HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 13 APRIL, 1940 No. 3

EFFECT OF BATHYPLECTES CURCULIONIS ON THE ALFALFA-WEEVIL POPULATION IN LOWLAND MIDDLE CALIFORNIA[1]

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Bathyplectes curculionis (Thomson)
Canidia curculionis Thomson 1887
Canidia subcincta[3] Holmgren 1858
Canidiella curculionis (Thomson) Dalla Torre 1891

INTRODUCTION

Bathyplectes curculionis (Thoms.), a larval parasite of the alfalfa weevil, was introduced into Utah from southern Europe by the United States Department of Agriculture Bureau of Entomology during the years 1911 to 1913, inclusive. Chamberlin (1924)[4] has given a brief account of the introduction and establishment of this parasite, and in 1926 he published further data on this subject and called attention to the rapid spread and increase of the species.

After the discovery of the alfalfa weevil in the lowlands of middle California in May, 1932, the Bureau of Entomology,[5] in 1933 and 1934, introduced *Bathyplectes* (fig. 1) into this new area.

In 1933 all liberations were made at Pleasanton, Alameda County, but in 1934 parasites were colonized in the San Francisco Bay area, Pleas-

[1] Received for publication April 7, 1938, but withdrawn to add 1938 data. Resubmitted March 25, 1939.

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[3] Preoccupied by *Campoplex* (= *Canidia*) *subscinctus* Gravenhorst 1829.

[4] See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.

[5] The Bureau of Entomology of the United States Department of Agriculture was combined with the Bureau of Plant Quarantine and became the Bureau of Entomology and Plant Quarantine on July 1, 1934.

anton, and in the San Joaquin Valley. In all localities *Bathyplectes* became readily established, and at the present time it can be found over the entire region infested by the alfalfa weevil. The rate of spread and the build-up of the parasite has been so rapid that it seems to be of sufficient importance to be discussed at this time.

W. B. Cartright of the Bureau of Entomology made the first recovery

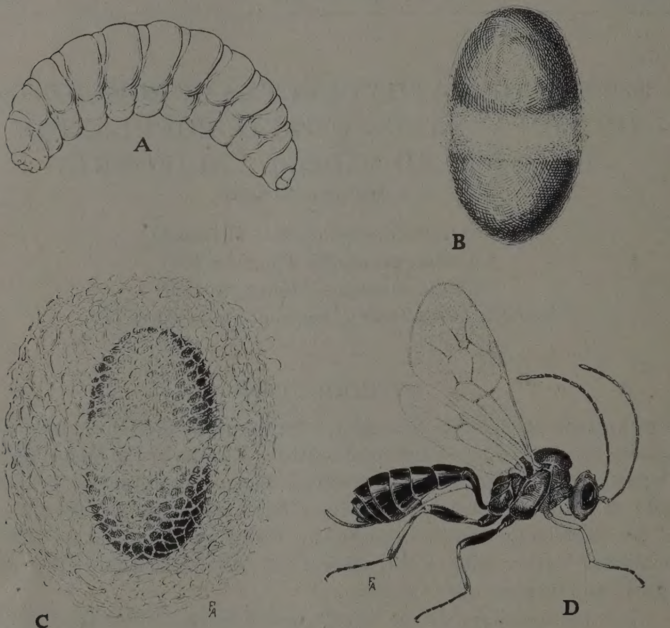

Fig. 1.—Life cycle of *Bathyplectes curculionis: A*, mature larva at time of leaving body of host; *B*, cocoon removed from within host cocoon; *C*, cocoon in normal position within cocoon of host; *D*, adult female parasite. (× 12.)

of the parasite on June 14, 1933, at Pleasanton, and on July 23, 1934, the author recovered the parasite for the first time in the San Francisco Bay area. No recoveries were made in the San Joaquin Valley until May 23, 1935, at which time about 30 per cent of the large alfalfa-weevil larvae were found to be parasitized.

While making a survey of the alfalfa fields at Pleasanton on May 15, 1935, a number of large alfalfa-weevil larvae were examined and most of them were found to be parasitized. It was decided then that if the

population trends of the alfalfa weevil were to be completely understood, it would also be necessary to gather information on the corresponding population trends of *Bathyplectes*. This marked the beginning of that study.

AREAS IN LOWLAND MIDDLE CALIFORNIA INFESTED BY THE ALFALFA WEEVIL

The infestation of the alfalfa weevil, *Hypera postica* Gyll.[6] (fig. 2), in lowland middle California occurs in three climatic zones, in each of which it behaves differently. These zones are designated as the San Francisco Bay area, the Pleasanton area, and the San Joaquin Valley area. The San Francisco Bay area includes the towns of Niles, Centerville, and Irvington; the Pleasanton area includes the agricultural region surrounding the town of that name; and the San Joaquin Valley area includes a rather large section of the northwest portion of that Valley. In the San Joaquin Valley, fields were examined on Union Island and in areas about the following cities and towns: Tracy, Vernalis, Westley, and Patterson. This includes the area of heaviest infestation in the Valley.

The San Francisco Bay area has a cool, moderate climate, which is in marked contrast to that of the hot, dry San Joaquin Valley. In the Bay area the mean summer temperatures are lower, and the mean winter temperatures higher than those in the San Joaquin Valley. The climate of Pleasanton is intermediate between these two. The response of the alfalfa weevil to these different climatic conditions is partially discussed by Michelbacher and Essig (1934*a*, 1934*b*, 1935). *Bathyplectes* is also influenced in a marked and distinct way by these climatic differences, and this study indicates that its effectiveness is influenced by temperature.

The alfalfa weevil also occurs outside of lowland middle California in the following counties: Alpine, Lassen, Modoc, Mono, Plumas, Sierra, and Siskiyou. The climate in these counties where the alfalfa weevil exists is similar to that found in the intermountain region of western United States. Because these localities are far removed from Berkeley, it was not feasible to carry on an investigation of the alfalfa weevil in any of them.

[6] Up to the present time the alfalfa weevil has been called *Phytonomus variabilis* Hbst. at this experiment station. However, in a letter from L. L. Buchanan to Dr. E. C. Van Dyke, dated June 20, 1939, Mr. Buchanan stated:

"I have been assembling a few notes regarding the nomenclature of *Hypera*, which, as you doubtless know, was improperly suppressed as a synonym of *Phytonomus* by Schoenherr in 1823 (Isis von Oken, column 1133). To some extent I have also examined the nomenclature of the alfalfa weevil, and cannot find any reason to reject Titus' conclusion that *postica* Gyll. should be used for this species, *variabilis* Hbst. 1795 having been previously used in the same genus by Fabricius in 1777."

It therefore appears that the correct name of the alfalfa weevil is *Hypera postica* Gyll.

EXPERIMENTAL METHODS

The method used in studying parasitism is briefly as follows: From various fields in the localities studied large numbers of nearly mature, last-instar larvae were collected by sweeping the alfalfa with an insect net.[7]

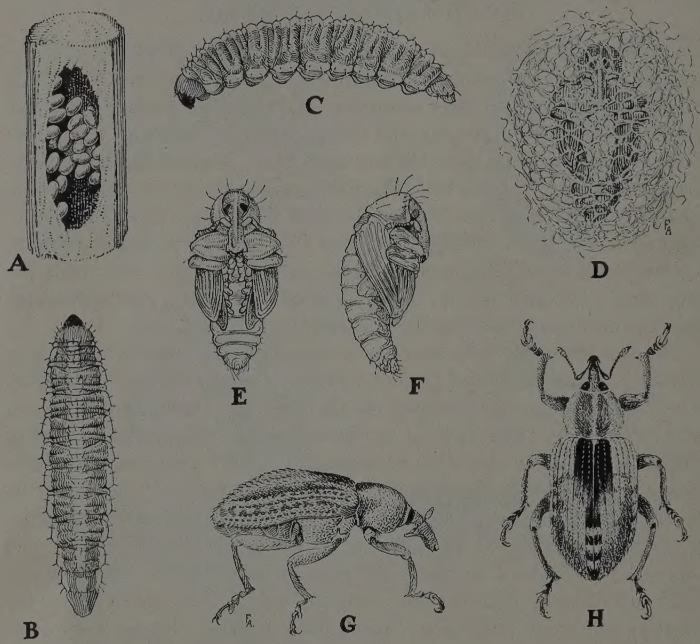

Fig. 2.—Life cycle of alfalfa weevil, *Hypera postica* Gyll.: *A*, alfalfa stem cut open showing a cluster of eggs; *B*, dorsal view of last-instar larva; *C*, lateral view of last-instar larva; *D*, pupa within lacelike cocoon; *E*, pupa removed from cocoon, ventral view; *F*, lateral view of pupa; *G*, lateral view of adult; *H*, dorsal view of adult. (× 6.)

These were taken into the laboratory where the parasites were reared. Frequently more than 500 host larvae were collected from a single field, and if possible not less than 100 were collected. Where the larval population was small, the larvae from several fields were sometimes grouped together. Often several thousand sweeps had to be made in order to obtain enough larvae for parasitism studies, and at times the larval popu-

[7] A number 5 "Harrimac" collapsing steel-frame landing net, manufactured by the Richardson Rod and Reel Company, Chicago, was used throughout this investigation.

lation dropped to such a low ebb that it was impossible to gather sufficient larvae for study.

It was decided to rear out the parasites rather than dissect them out because this less tedious and time-consuming method made it possible to study a larger number of fields and to base the percentage parasitized on a greater number of individuals. Early in the investigation these two methods were compared, with the result that the percentage parasitized obtained by rearing was slightly greater than that shown by dissection. However, no note was made of host larvae containing eggs of the parasite,

TABLE 1

PER CENT OF LAST-INSTAR ALFALFA-WEEVIL LARVAE PARASITIZED BY *Bathyplectes curculionis* AS DETERMINED BY DISSECTION AND BY REARING, 1935

Location	Date	Dissection			Rearing		
		Number of larvae dissected	Number parasitized	Per cent parasitized	Number of hosts	Number parasitized	Per cent parasitized
Pleasanton:							
Field 1.............	May 23	38	36	94.7	—*	—	—
Field 2.............	May 23	100	80	80.0	—	—	—
Field 3.............	May 23	200	165	82.5	157	155	98.7
	May 31	200	192	96.0	143	139	96.4
	June 3	100	94	94.0	80	75	93.7
Irvington...........	June 3	87	77	88.5	69	66	95.6

* Dashes indicate data not available.

and because of the possibility of overlooking some recently hatched parasites, it can be assumed that the two methods would give comparable data. The comparative results obtained are shown in table 1. Obviously, the rearing method has several disadvantages, among which are: (1) Some of the larvae collected do not spin their cocoons for from 1 day to several days, which means that the total time they would have been subject to an attack by the parasite is reduced by that number of days. This probably is not a serious objection to the method, for Reeves and Hamlin (1931*b*) stated that doubtless because of their tough skin, last-instar larvae are exceptionally free from attack by *Bathyplectes*. (2) Some of the weevil larvae die, and it is impossible to determine whether or not they were parasitized. For this reason dead individuals were discarded, and the percentage parasitized was based upon the number of parasites and hosts recovered.

Usually the examinations were made about 10 days after the collections were brought into the laboratory. By this time practically all the parasites had emerged from their hosts and spun cocoons within those

made by the weevil larvae. The weevil larvae collected were placed in one section of a moisture dish with fresh alfalfa and covered with a cloth. The progress of the culture could be determined by looking through the bottom of the dish where many of the weevil larvae moved before spinning their cocoons.

ALFALFA-WEEVIL-POPULATION TRENDS

Before considering parasitism further the seasonal trends of the alfalfa weevil will be briefly discussed. This insect responds differently to environmental conditions in California and in the Great Basin.

In the Great Basin area most of the overwintering alfalfa-weevil adults lay their quota of eggs on the first crop of alfalfa, but according to Reeves and Hamlin (1931*a*) there are a few overwintering adults that survive to lay eggs on the second crop. They also state that the individuals arising from these eggs may be the important ones in carrying the weevil over to the following year. Not only do they escape parasitism, but their development is so rapid that a large percentage of the larvae that mature on the second crop of alfalfa pupate and emerge before cultural kill comes into play at the second cutting. They believe that these adults serve to maintain the weevil at an economically dangerous level. According to their investigations, the population that arises from the first crop is largely destroyed by parasitism and cultural kill. This was substantiated by Newton (1933), who further stated that there is some scattered egg laying throughout the season until winter. On the other hand, in a later paper Hamlin *et al.*[8] point out that when parasitism is low and cultural kill ineffective on account of adverse weather conditions at first harvest, the bulk of the new adults may be produced from the first-crop larvae.

Here in middle California egg laying takes place early, and maximum alfalfa-weevil-larval populations occur from the latter part of March to the first part of May, according to weather conditions. Typically, in individual fields the largest larval population occurs on the first crop, although there are numerous cases where the highest population occurs on the second crop, and sometimes even later than this. In nearly all cases there are surviving overwintering adults that lay eggs on the second crop, but the numbers that occur here largely depend on the time of cutting the first crop. If the first cutting is premature, a fairly large larval population can be expected on the following crop. A young vigor-

[8] According to correspondence by John C. Hamlin and Ralph W. Bunn to author, May 16, 1938, in which they summarize a part of a manuscript, "Bionomics of the alfalfa weevil" now in the course of preparation; the manuscript was not seen by the present author.

ous stand of alfalfa may reach maturity in a relatively short period and be cut long before the overwintering adults have depleted their egg supply. If cutting the first crop is greatly delayed, the overwintering adults will nearly finish egg laying before cutting. This relation of overwintering adults to the time of cutting the first crop must be more or less the same wherever the weevil occurs.

In California another complication is that current-season adults reach sexual maturity during late spring and summer. Because of this, a second build-up in the larval population may take place from the latter part of June throughout most of July. Prior to this rise, the larval population usually reaches a very low point. The second peak generally occurs on the third crop although it may be delayed until the fourth, and occasionally in individual fields it may exceed the peak that occurred on the first crop.

To what extent the current-season adults reach sexual maturity is probably largely dependent upon climatic conditions. Evidence which shows that current-season adults reach sexual maturity is reported on by Michelbacher and Essig (1935). Apparently the hot temperature that occurs as summer progresses either slows down or inhibits sexual development of the adult weevils, for otherwise higher larval peaks could be expected. That this should occur is not surprising because the alfalfa weevil is an insect that prefers cool weather, as is indicated by its stimulation to activity early in the year. Possibly high temperatures send the adults into semi-estivation, and this is more marked in the San Joaquin Valley than in the cooler San Francisco Bay area.

SEASONAL HISTORY OF BATHYPLECTES

Bathyplectes normally produces two generations a year, the short- and long-cycle cocoons. The long-cycle cocoons have thicker walls, are darker in color, and contain the overwintering forms. At about the time the alfalfa begins growing in winter or early spring, adult parasites emerge from these cocoons and oviposit in the alfalfa-weevil larvae that occur from an early hatching of eggs. The parasites complete their larval development in a short period, and upon emerging from their hosts spin the light-colored, short-cycle cocoons. The adults emerge from these cocoons very soon and oviposit in the weevil larvae, which have become abundant by this time. When these parasites complete their larval development, they emerge from their hosts and spin the dark, thick-walled, long-cycle cocoon.

The seasonal history as outlined above does not occur in lowland mid-

dle California.[9] Both types of cocoons are produced, but not at definite periods. *Bathyplectes* adults emerge during January and probably on through March, the duration of the emergence depending upon weather conditions. Large numbers of overwintering forms were reared at Berkeley in 1935 and were stored on a window sill having a north exposure. There was no heavy emergence from these until January, 1936. The overwintering forms reared in 1936 were kept in the same location, and adults did not emerge until late in January, 1937, the later emergence probably being due to the very cold weather that prevailed during the first part of that year. Emergence from this group lasted from January 11 to April 1.

The period of emergence coincides rather closely with the time that the weevil is stimulated to activity. The *Bathyplectes* adults from the overwintering cocoons oviposit in the early alfalfa-weevil larvae, but their progeny consists of both long- and short-cycle cocoons. Apparently the long-cycle individuals will not emerge until the following season. From collections of parasitized larvae made throughout the season, some cocoons of both cycles were usually obtained. The overwintering cocoons were present in fairly large numbers, but, as the season progressed, they appeared in smaller numbers until April, when the proportion of overwintering cocoons rapidly increased again, until by the end of May most of the parasites were overwintering forms.

The approximate trend in the production of overwintering forms in the San Francisco Bay area and in the San Joaquin Valley for 1937 is shown in figure 3. This information was obtained from the field collections of alfalfa-weevil larvae brought into the laboratory for parasitism studies, which are discussed in the next section. The points plotted are the average percentages of cocoons overwintering obtained from those collections. The term "approximate trend" is used because only those cocoons known definitely to be overwintering cocoons were used in calculating the percentage figures. Poorly formed cocoons or larvae that failed to spin cocoons were placed with the short-generation group. Therefore the percentage of cocoons overwintering should be slightly higher than that shown in the figure. The two curves are based on rearing records from last-instar-weevil larvae brought into the laboratory. The change to laboratory conditions might produce different results from those of field

[9] Hamlin *et al.* (see footnote 8, p. 86) call attention to the fact that there are not two complete generations of the parasite in the Great Basin—only a partial second generation. Their work has shown that all the overwintered individuals do not produce the short-cycle cocoons; some produce long-cycle cocoons immediately and thus have only one generation. They state that the percentages responding in these two ways are not known. The development as they have given it agrees rather closely, but not entirely, with that which occurs in lowland middle California.

conditions. In fact, some evidence was obtained which indicated that under the warmer conditions of the laboratory more overwintering forms are produced than would be expected under field conditions. Similar data were collected in 1936, but this material cannot be included, for early in the season no accurate count was made of the overwintering cocoons. The results, however, are similar to those obtained in 1937. In the

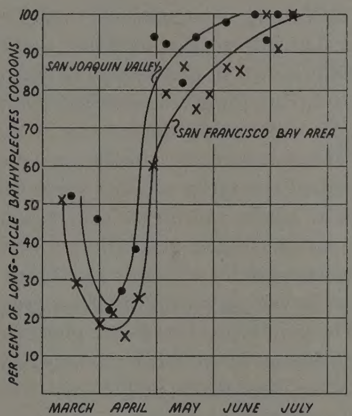

Fig. 3.—Production of long-cycle, or overwintering, *Bathyplectes curculionis* cocoons in the San Joaquin Valley and in the San Francisco Bay area in 1937.

San Joaquin Valley the activity of the parasite is more limited than in the San Francisco Bay area. Apparently the hotter climate of the Valley tends to cause the production of overwintering forms to a greater degree than the cooler climate found about the Bay area. This might account for the fact that the parasite is less effective in the San Joaquin Valley.

During the summer and fall of 1935 any large collection of alfalfa-weevil larvae in the San Francisco Bay area contained some that were parasitized. When the collection of parasitized larvae was large, some of these were almost certain to be short-cycle individuals. During the summer and fall it was not uncommon to collect adult *Bathyplectes* in the field. These same conditions were observed during 1936 but to a much smaller degree. For summer and fall activity of *Bathyplectes* to be noticeable, apparently two conditions are necessary, namely : a certain host density and a cool climate.

PARASITISM TRENDS IN THE DIFFERENT CLIMATIC ZONES

Bathyplectes curculionis, as has already been suggested, is apparently very much influenced by climate, and its reaction under one set of conditions cannot be taken as an indication of its behavior under different conditions.

A large mass of information has been collected on both parasitism and the trends of the alfalfa-weevil populations in the three climatic areas under consideration. The information obtained for the different areas is plotted by years and is shown in figures 4 to 6. Larvae and adults were collected at intervals during the growing season by sweeping the alfalfa with an insect net. Except during the growth of the first crop alfalfa fields were seldom swept before the alfalfa was one-fourth grown. In each of the fields studied two series of 100 sweeps each were made, and the average number of adults and larvae collected per 100 sweeps was used as a population index. On each graph the population figures (larvae and adults) are the averages for all fields in a given area, and the percentage of last-instar larvae parasitized is the average for several fields in the same area.[10] The population trends are plotted only through October, although in some seasons in the San Francisco Bay area and adjacent areas it was possible to collect adults and larvae of the alfalfa weevil by sweeping during all months of the year.

On the graphs only averages for all fields are shown, but frequently a wide range[11] in larval and adult populations was found while making the sweeps. In some fields very few larvae were collected, whereas in others the number collected was large. For example, in the San Joaquin Valley on March 20, 1934, only 2 larvae per 100 sweeps were collected in one field. In another field on that same day 1,194 larvae per 100 sweeps were collected. The average (six fields) shown on the graph was 302. In the San Francisco Bay area on March 21, 1934, the range was from 50 to 1,609 larvae per 100 sweeps, with an average (six fields) of 601. A few days before—March 15, 1934—in the Pleasanton area the range was 67 to 516 larvae per 100 sweeps, with an average (six fields) of 257.

[10] It is recognized that from a statistical standpoint average percentages as computed here, in which all fields are given equal weight, might in some cases give misleading results. In this particular case, however, average percentages determined in this way have been checked against those determined by grouping the larvae, total and parasitized, from all fields and then computing the average parasitism. The discrepancy is so slight as to have no significance.

[11] The data for low, high, and average larval and adult alfalfa-weevil populations and percentage of last-instar larvae parasitized by *Bathyplectes* were tabulated for the three infested areas for the period 1933–1938, but because the data duplicated the graphs in part, they have not been included. These tables have been included with the progress report and can be consulted in the files of the Division of Entomology and Parasitology, College of Agriculture, University of California, Berkeley.

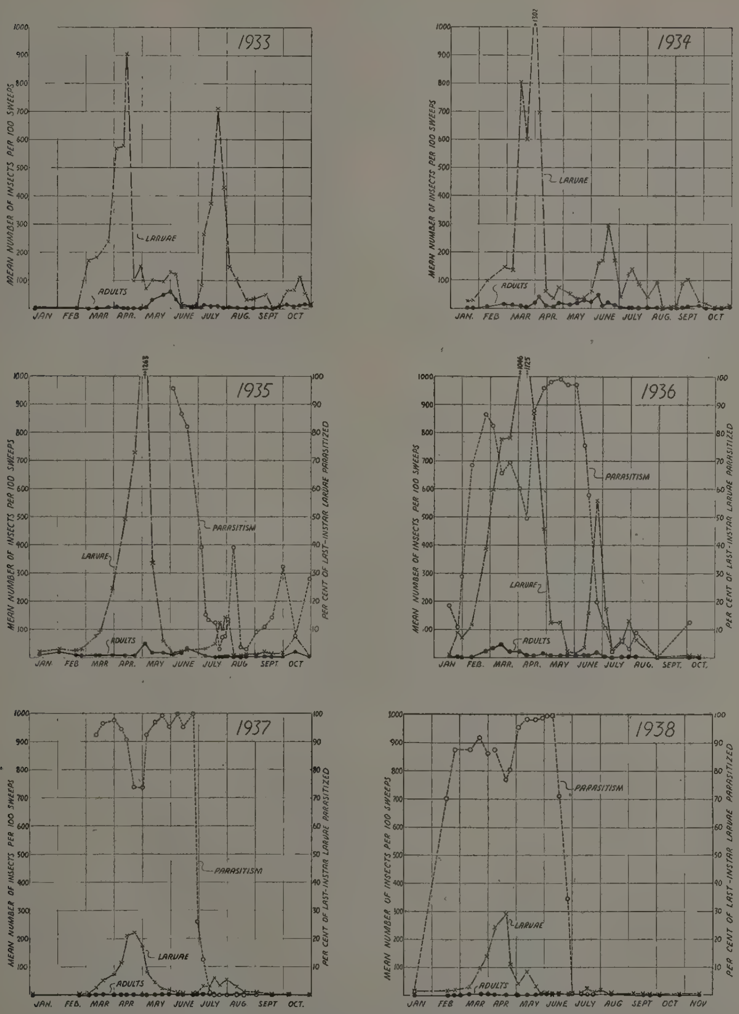

Fig. 4.—Alfalfa-weevil population and parasitism in the San Francisco Bay area, 1933–1938: average number of larvae and adults collected per 100 sweeps of an insect net, and percentage of last-instar-weevil larvae parasitized by *Bathyplectes curculionis.* Parasites were introduced in 1934.

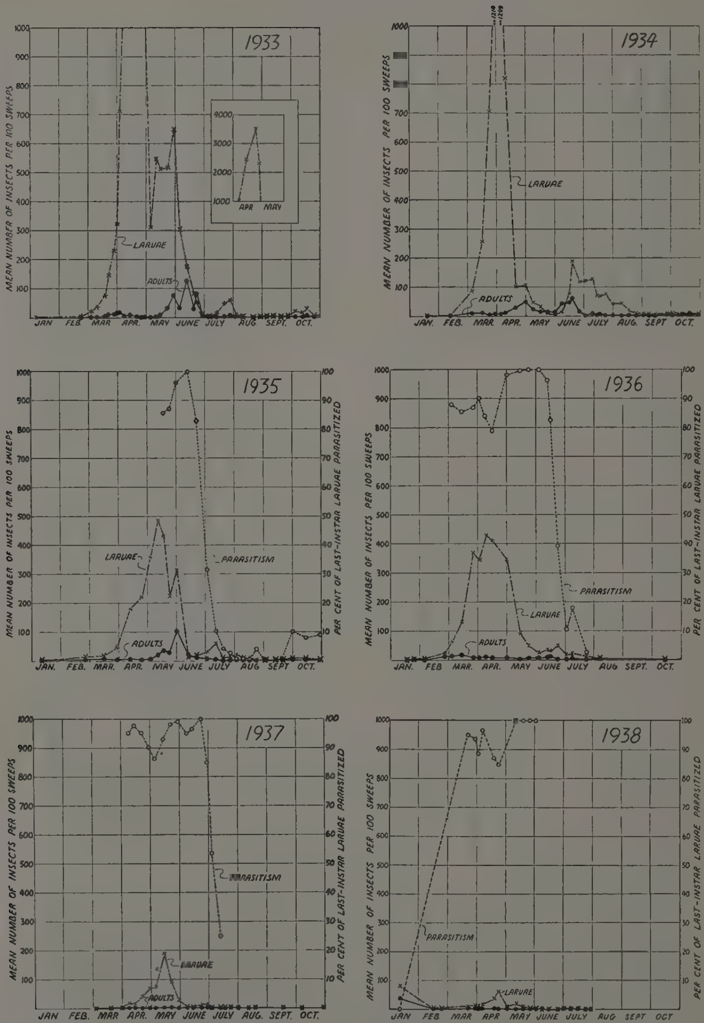

Fig. 5.—Alfalfa-weevil population and parasitism near Pleasanton, 1933–1938: average number of larvae and adults collected per 100 sweeps of an insect net, and percentage of last-instar-weevil larvae parasitized by *Bathyplectes curculionis*. Parasites were introduced in 1933.

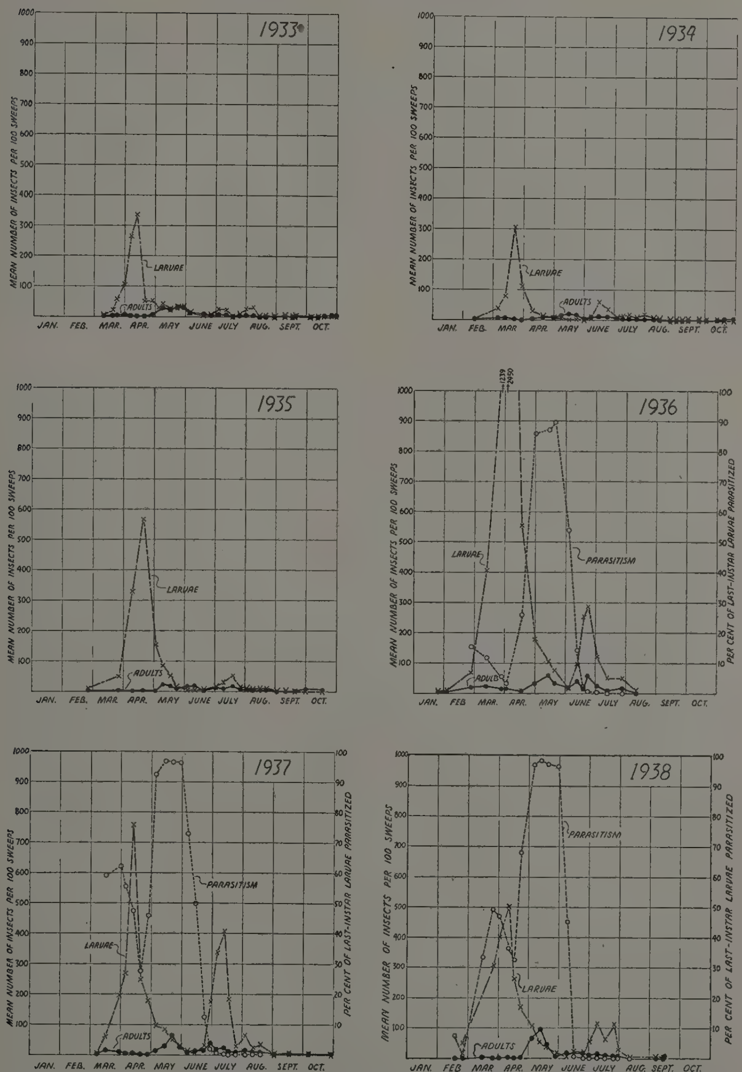

Fig. 6.—Alfalfa-weevil population and parasitism in the San Joaquin Valley, 1933–1938: average number of larvae and adults collected per 100 sweeps of an insect net, and percentage of last-instar-weevil larvae parasitized by *Bathyplectes curculionis*. Parasites were introduced in 1934.

An examination of the graphs shows that in the winter *Bathyplectes* begins to emerge and to lay eggs at about the same time that the weevil becomes active. In general the percentage parasitized increases at first, but after a given time, which coincides with the last period of rapid host increase, the curve turns downward. This downward trend is then arrested owing to either one or both of the following reasons: the cutting of the first crop or the emergence of the short-cycle parasite. The next rise is very abrupt and the percentage parasitized remains close to 100 per cent for a considerable time; then it drops off sharply and may even fall to zero. The extent of this fall depends largely upon climate and host abundance. The alfalfa-weevil larvae of the second crop are highly parasitized, which is just the reverse of what occurs in the Great Basin (Reeves and Hamlin, 1931*a*; Newton, 1933).

The year 1936 was one of the most favorable encountered for a build-up in the weevil population. There was a marked increase in the population in the San Joaquin Valley. In the San Francisco Bay area the population remained about constant, while at Pleasanton an actual decrease occurred. Possibly in the last two named areas *Bathyplectes* played an important rôle in holding down the weevil population. If this were the case, it would seem from a study of the graphs for 1936 that the parasite was most effective at Pleasanton, somewhat less so in the San Francisco Bay area, and of little importance in the San Joaquin Valley. In the Pleasanton area parasitism remained high during the entire period that alfalfa-weevil larvae could be easily found. In the San Francisco Bay area a considerable number of the first-crop alfalfa-weevil larvae escaped parasitism, and also later in the season after parasitism had dropped off abruptly, a considerable number of larvae were not parasitized. In the San Joaquin Valley most of the first-crop larvae escaped parasitism, and while those of the second crop were heavily parasitized, the large number of weevil larvae that came on later escaped parasitism altogether. Thus only a very small percentage of the total host population in the San Joaquin Valley was parasitized.

The 1937 season was not nearly so favorable for the weevil as was the preceding year, and there was a marked falling off of the weevil population throughout the three areas. With this decline in the weevil population, *Bathyplectes* appeared to play a more important rôle than it did in 1936. Early throughout the infested areas *Bathyplectes* adults were emerging in fairly large numbers before weevil larvae were plentiful. The adult parasites were most abundant in the San Francisco Bay area. On February 22, in one field the average number of *Bathyplectes* collected per 100 sweeps was 11½, while the average number of hosts was

only 1½. Eight days later the ratio was 42 to 14. In this area parasitism was heavy until nearly the first of July. After this period there was a slight build-up in the alfalfa-weevil-larval population, and these individuals for the most part escaped parasitism. At Pleasanton parasitism continued high until the first of July. This period included the entire time that the alfalfa-weevil larvae could be collected in any quantity. In the San Joaquin Valley the percentage parasitized was greater than in the preceding year but did not compare favorably with that at Pleasanton and in the San Francisco Bay area. Many of the first-crop larvae escaped parasitism, as did practically all of those occurring on the third and later crops. Parasitism began to fall off rapidly at a considerably earlier date in the San Joaquin Valley than in either of the other two areas.

There was one field at Patterson, in the San Joaquin Valley, in which the weevil population had built up to a point so that it greatly exceeded the populations in any of the surrounding fields in the same locality. For example, on April 5, 1937, the average larval count for this field was 963, while a field less than a quarter of a mile away had an average count of 215. Other fields only a few miles distant showed even a lower count. The highest count observed in this field in 1936 was 5,893 larvae to the 100 sweeps, as compared to 2,542, the larval count in the next most heavily infested field. In 1937 the maximum larval count obtained in the Patterson field was 2,072, while the next highest count was only 480. The Patterson field has been included in the graphs for the years 1936 and 1937. The inclusion of this field has not changed the shape of the curves to any great extent. It has tended to increase the height of the larval curve and to lower the parasitism curve. Further, if the field were excluded from the 1937 graph, the curves would be similar to those for 1933 and 1934 except for the high larval peak that occurred in July, 1937. This peak was the result of a high larval count in a single field, all other fields used in this investigation having been recently cut. Also the inclusion of the Patterson field tends to convey the idea that the average larval population in the San Joaquin Valley is larger than it really is. On the whole the larval count in the fields in the San Joaquin Valley is relatively small. Figure 7 shows graphs for the San Joaquin Valley with the Patterson field excluded.

In the San Francisco Bay area the weevil population remained rather constant until 1937 when there was a sharp drop. A portion of this decline was undoubtedly due to climatic conditions, although *Bathyplectes* was partly responsible.

In early January, 1938, alfalfa-weevil larvae were collected in the fields about the San Francisco Bay and at Pleasanton. At that time *Bathyplectes* adults were scarce and parasitism was very low. In one

field at Pleasanton an average of 37 adult alfalfa weevils was collected to the 100 sweeps, and certainly this should have indicated a large larval population later on. However, shortly after the survey was made (January 11), there were heavy rains, and this particular area was flooded for weeks. This resulted in killing the alfalfa as well as the weevil. Apparently this was the only area where the weevil held any threat; for the entire year the weevil population encountered was the smallest since the investigation was started. The parasitism trend was similar to that encountered in 1936 and 1937. It is regretted that the field that showed the

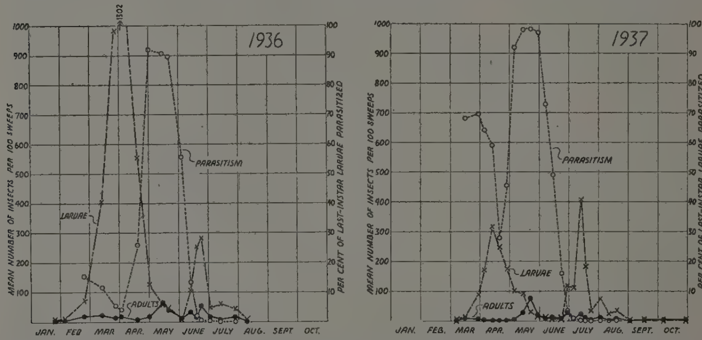

Fig. 7.—Alfalfa-weevil population and parasitism in the San Joaquin Valley, 1936–1937: average number of larvae and adults collected per 100 sweeps of an insect net, and percentage of last-instar-weevil larvae parasitized by *Bathyplectes curculionis*. The data on the heavily infested field at Patterson have been excluded.

heavy adult-weevil population was flooded. If this had not occurred, there would probably have been a rather heavily infested field in an area where the weevil has been relatively scarce for a number of years. This has led the author to believe that in the area about Pleasanton occasionally alfalfa fields will be found in which the weevil may be slightly destructive.

In the San Francisco Bay area and in the San Joaquin Valley the 1938 weevil-population trends and amount of parasitism were rather similar to those found in 1937. The evidence certainly indicates that *Bathyplectes* is playing an important rôle in limiting the alfalfa weevil in the San Francisco Bay area. On the other hand, although parasitism by *Bathyplectes* may be important in the San Joaquin Valley, it is certainly not as effective in controlling the weevil as it is in the cooler areas. In the San Joaquin Valley one field was rather severely injured by the alfalfa weevil, and rather high larval populations were encountered in one or two others fields.

In general, for the three years 1936 to 1938, the results of this study indicate that *Bathyplectes* will be most effective in the cooler weevil-infested areas. As with the alfalfa weevil, moderately cool temperatures seem to favor it more than warmer temperatures. For that reason its active period is of longer duration in the San Francisco Bay area than in the San Joaquin Valley.

EFFECTIVENESS OF PARASITISM

Bathyplectes curculionis has been present in lowland middle California for too short a time to make any definite prediction concerning its final effect upon the weevil population. Certainly at the present time (1938) it shows considerable promise, and if parasitism continues as high as in the past, *Bathyplectes* should prove to be an extremely valuable parasite. Frequently, however, an insect introduced into a new area builds up in tremendous numbers for a few years, then decreases in number and finally comes to equilibrium with the environment at a much lower level than that at the beginning. *Bathyplectes* may behave in this way. However, the following points are in favor of its becoming an effective parasite: the ease with which it finds its host, the percentage of hosts accessible to attack (that is, in the larval stage), the rapidity of its multiplication, and its facility for rapid dissemination.

At Pleasanton from 1932 to 1938 there has been a great decrease in the weevil population. Both adult and larval numbers have been reduced to a very low ebb. A portion of this decline has been due to better cultural care, some probably to climate, and a large part due to the establishment of *Bathyplectes*. If this area is compared with the others, *Bathyplectes* would appear to be the most important influence in bringing about the decline in the weevil population, but there is danger in reaching such a conclusion. During the same period that the weevil population was declining at Pleasanton it was increasing in the San Joaquin Valley, although a sharp decline occurred there in 1937. The build-up of the weevil in the San Joaquin Valley is believed by the author to be due to favorably climatic conditions and not the result of its being recently introduced into that area.

The alfalfa weevil has not been studied over a sufficiently long period in the infested area of lowland middle California to know the exact fluctuations that might occur in the weevil's population because of meteorological variation. For example, had the conditions in the San Joaquin Valley been reversed so that instead of low populations during the first years of this investigation there had been high ones, the decline in the population in the succeeding years might have been attributed to the in-

troduction of *Bathyplectes*, which of course would have been false. Certainly, up to the present time all the data indicate that *Bathyplectes* will be least effective in that area. However, where parasitism has been as complete as it has been in the Bay area and at Pleasanton, the only reasonable belief is that some few individuals die as a result of parasitism that would otherwise escape death from other causes. If this is the case, and as evidence certainly indicates, *Bathyplectes curculionis* will be an important factor in reducing the alfalfa-weevil population in those areas where its activity is prolonged.

SUMMARY

Bathyplectes curculionis (Thoms.), a larval parasite of the alfalfa weevil, was introduced into lowland middle California by the United States Department of Agriculture Bureau of Entomology during the seasons of 1933 and 1934. It became readily established and was recovered at Pleasanton on June 14, 1933, and in the San Francisco Bay area on July 23, 1934. It was not found in the San Joaquin Valley until May 23, 1935, at which time about 30 per cent of the large alfalfa-weevil larvae were found to be parasitized.

Parasitism studies were conducted in three different climatic areas: the San Francisco Bay area, Pleasanton, and the northwest portion of the San Joaquin Valley.

Parasitism was determined by making field collections of last-instar alfalfa-weevil larvae and rearing through the parasites in the laboratory.

In each field two lots of 100 sweepings were made with an insect net, and the average number of larvae and adults collected per 100 sweeps was used as a population index for the alfalfa weevil.

The highest alfalfa-weevil-larval peak generally occurs on the first crop, but it may occur on the second or even later crops. Weevil activity begins early in the growing season, and a second generation generally makes its appearance during the latter part of June and through July.

Bathyplectes curculionis produces short- and long-cycle forms. Individuals of the latter form are produced at any time during the active period of the parasite. Climate apparently greatly influences the behavior of *Bathyplectes*. Its active period is limited by the hot climate of the San Joaquin Valley. In the cooler portions of the weevil-infested areas of lowland middle California the parasite is able to continue activity throughout the growing season. The most active period ranges from early season until about the first of July. For summer and fall activity to be noticeable two conditions are apparently necessary, namely: a certain host density and a cool climate.

The information gathered concerning parasitism and alfalfa-weevil-population trends is shown by graphs for the different regions studied. The graphs clearly indicate that the San Joaquin Valley is less suited to *Bathyplectes* than the cooler areas.

Definite predictions concerning the final effect of *Bathyplectes* upon the alfalfa-weevil population cannot be made as yet, but at the present time (1938) the parasite shows considerable promise. From all indications, it will certainly exert a marked controlling influence in the cooler weevil-infested areas.

ACKNOWLEDGMENTS

Many thanks are due to Professor Harry S. Smith for his suggestions on conducting the investigation and on interpreting the data included in this paper; also to Professor E. O. Essig, under whose supervision much of the work was done.

The author is under obligation to the W.P.A. for the assistance given in the carrying out of this investigation.

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THE APPARENT CLIMATIC LIMITATIONS OF THE ALFALFA WEEVIL IN CALIFORNIA

A. E. MICHELBACHER AND JOHN LEIGHLY

THE APPARENT CLIMATIC LIMITATIONS OF THE ALFALFA WEEVIL IN CALIFORNIA[1]

A. E. MICHELBACHER[2] AND JOHN LEIGHLY[3]

INTRODUCTION

THE ALFALFA WEEVIL, *Hypera postica* Gyll.,[4] was first discovered in lowland middle California in 1932. The extent and direction of its spread from its original areas are shown on the map in figure 1. The expansion of the area of infestation has been slight in view of the rapidity of spread of the insect that has been reported from other parts of the United States. Along some parts of the periphery of the area of infestation a slow rate of spread may possibly be the result of absence of suitable and abundant host plants. But in one sector of the periphery of the infested area—in the northwestern San Joaquin Valley—the boundary cuts across a continuous area devoted to the cultivation of alfalfa, where any insect preying on alfalfa might be expected to be disseminated rapidly and continuously from field to field. As may be seen from figure 1, no such spread has been observed. There appears to be no good reason why the southward spread of the insect is checked here unless it encounters a climatic barrier. Southward in the San Joaquin Valley summer temperatures become steadily higher; and all investigations of the alfalfa weevil indicate that high temperatures check the activity of the adult weevil and eventually inhibit its activity altogether.

The existence of an apparent climatic limit to the southward spread of the weevil in the San Joaquin Valley, and the reasonable conclusion that the climatic barrier encountered is high summer temperature, are the considerations that have prompted the investigation reported in this paper. Since the weevil is of rather recent introduction in California, it appeared that some light might be thrown on this question by a study of the temperatures obtaining in its original habitat in the Old World, with particular attention to the southern limit of its distribution there. The conclusions arrived at through this comparative study of the dis-

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[4] Formerly called *Phytonomus variabilis* Hbst.; see footnote 6, p. 83, in the accompanying paper (Michelbacher, 1940).

tribution of the insect and the temperatures that obtain along the limits of the areas infested by it are finally used in an attempt to predict approximately its possible future spread in California.

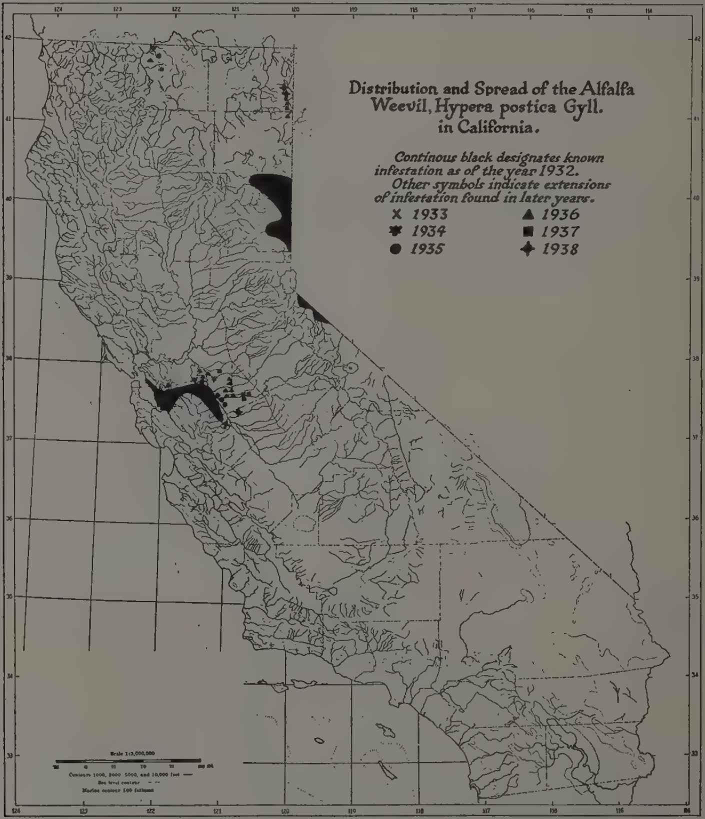

Fig. 1.—Areas in California infested by the alfalfa weevil in 1932 and the spread of the insect since that year.

SEASONAL ACTIVITY OF THE ALFALFA WEEVIL IN RELATION TO TEMPERATURE

A review of the seasonal history and habits of the alfalfa weevil appears necessary for an understanding of the climatic relations of its activity in California and elsewhere. Probably the most important consideration

is that a female weevil on emerging from its cocoon is not sexually mature; several months must pass before it is capable of laying eggs. The length of this diapause is variable and is greatly influenced by temperature. Snow (1928)[5] conducted a careful investigation and found that the shortest time necessary for adults to reach sexual maturity is at least 4 months. Yakhontov (1934) gives the time as 55 to 60 days where the temperature does not fall below 12° C or rise above 25°. Observations in California indicate that some individuals reach sexual maturity within a 2-month period. Snow's work was done in the Great Basin, where sexual maturity is probably retarded by the high temperature to which the weevils are subjected upon their emergence from the cocoons.

In lowland middle California the first generation comes early, and consequently the emergence of new adults occurs before really hot weather sets in. The majority of the adults emerge in April, some even earlier. Therefore, the temperatures prevailing immediately after their emergence are highly satisfactory, and the length of the diapause is relatively short. The earliness of the first generation can probably be best appreciated by noting that the larval peak is reached in lowland middle California (fig. 4) at about the time that temperatures favorable for adult activity are beginning to occur in the Great Basin. In the intermountain region, which includes the Great Basin, most of the adults emerge in June and July; and the temperatures that obtain during these months and for a time thereafter are sufficiently high to lengthen greatly the diapause, and therefore a number of months must pass before sexual maturity is reached. Except for the fact that the alfalfa weevil is slow to reach sexual maturity, it would probably be a more serious pest in California and possibly elsewhere than it actually is.

Although the study of the weevil at this station has been in progress only since 1932, there is already considerable evidence that many adults of the first brood of larvae reach sexual maturity and lay eggs before the summer is past. Overwintering adults usually lay most of their eggs on the first crop of alfalfa, although a certain number lay eggs on the second crop. By the time the third crop starts its growth, however, the overwintering adults have nearly depleted their egg supply and larvae are very difficult to find. Toward the end of June there may be a marked increase in the larval population; in certain fields the larval population has at times exceeded that of the first crop. This increase can be accounted for only by supposing that some of the adults of the current season's generation have reached sexual maturity and are giving rise to a second

[5] See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.

generation. This occurs for a certainty in the cooler parts of lowland middle California, as is shown by experiments in which larvae, caged outdoors, pupated, emerged, and produced progeny during the same season (Michelbacher and Essig, 1935).

Probably the second generation makes it possible for the alfalfa weevil to establish relatively large populations in certain fields. Apparently exceptionally favorable conditions are necessary for this to occur. For example, a field with a comparatively low population density may change to one with a high density if weather conditions are such that a large number of adults of the current season's brood are able to reach sexual maturity before hot weather sets in. These adults must, moreover, reach sexual maturity and begin depositing eggs at the time when a new crop of alfalfa starts its growth; for if this condition is not fulfilled, the alfalfa will be cut and the new generation of weevils will die by cultural kill before they have had a chance to complete their development. This is what usually occurs; and by the time the next crop of alfalfa starts its growth, temperatures have risen high enough to send nearly all the adults into estivation. If a field once becomes heavily infested, however, favorable circumstances thereafter are likely to permit the expansion of the weevil population to a density that will be destructive as long as the field is left in alfalfa.

Because of their much later emergence in lowland middle California, we are inclined to believe that relatively more adults of the second brood survive the summer than do the adults of the first brood. It seems highly possible that there must be a certain mortality among the adults of the early brood before the adults of the second generation have emerged. Also, the first brood gives rise to the second, and therefore many of the individuals of the first brood must begin the summer in at least a partially depleted condition. The adults of the second brood may be comparable to the first and only brood of adults that occurs in the Great Basin; for in both cases they emerge at about the same time of the year. The only marked difference is that in California the adults have to withstand higher summer temperatures than in the Great Basin.

CLIMATIC CONDITIONS UNDER WHICH THE ALFALFA WEEVIL EXISTS

Summer Temperature as a Limiting Factor.—The aim of the present paper—to estimate from the present climatic distribution of the alfalfa weevil its probable future spread—is similar to that of an earlier paper by Cook (1925). Since, however, this paper is concerned with a smaller

and climatically more homogeneous area than Cook discussed, the procedure is more detailed and has been determined by close observation of the seasonal history of the insect in lowland middle California. This paper deals, moreover, with the southern limit of dispersal of the insect, with which Cook, for lack of observational data, did not concern himself. His immediate acquaintance with the weevil was gained in the northern part of the intermountain region of the United States, where cold and wet spring weather and low winter temperatures are demonstrably limiting factors in the survival of the weevil. He was led, therefore, to attach great weight to precipitation as a climatic factor, since a moist habitat favors certain entomophagous fungi that attack the larvae of the weevil. This line of reasoning led him to conclude that almost the whole of California, with its dry summers, was destined to become an area of "normal occurrence" of the insect. He did, however, consider it possible "that the high temperatures of southern California and Arizona may prove fatal to larvae."

Any climatic limitations on the spread of the weevil in lowland middle California must be imposed by summer temperatures, not by precipitation. We have therefore ignored precipitation in interpreting present distribution and future spread of the weevil in California. Our method of handling climatic data is much closer to Yakhontov's (1934) than to Cook's. Like Cook, Yakhontov knows best the northern limit of the weevil (in the U. S. S. R.), but he has shown that this northern limit may very well be defined by temperatures alone.

Among investigators of the weevil there is general agreement on the gross relations of its activity to temperature. Moderately cool weather is favorable to its activity. There is no definite hibernation; it is active when warm and quiet when cold (Reeves, Miles, *et al.,* 1916; Yakhontov, 1934). According to Sweetman (1929) the weevil becomes active when the temperature rises to about 10° or 12° C. Regarding the upper temperature limit of its activity. Sweetman and Wedemeyer (1933), working under controlled conditions, found that the upper limit of the range of temperature favorable to oviposition is approximately 28° C. Yakhontov (1934) states that the insect does not become active until a temperature of 12° C is reached, and that a temperature of 25° limits the activity of the adult. His investigations showed that 55 to 60 days are required for the development of the internal reproductive system, and that a temperature higher than 12° C but lower than 25° is necessary for this development. In working out the climatic limitations of the insect he found it necessary to add to the period required for the weevil to pass through the developmental stages (from the egg to the emergence of the adult) a period of 55 to 60

days to allow the adults sufficient time to reach sexual maturity. He computed the period suitable to the weevil as beginning when the daily mean temperature reaches 10° C. This is apparently a rather satisfactory starting point, since, with such a mean temperature, the temperature during a part of the day will ordinarily be in excess of 12° C. The temperatures selected by Yakhontov come close to defining the range within which the adult weevil is active and are used here in a slightly modified form as the basis of our attempt to determine the southern limit of distribution of the insect.

The temperatures used by Yakhontov and those which must be used in the investigation of the distribution of any organism in relation to climate are climatologic temperatures, not controlled laboratory temperatures. That is to say, they are observed in standardized ventilated shelters several feet above the ground. Observations thus made obviously do not record the temperature of the air within the stand of alfalfa infested by the insect, the temperature of the plants, nor the temperature of the bodies of the insects themselves. The temperatures actually experienced in the field by the insects are not known. It cannot be doubted, however, that at midday and in summer the temperatures to which insects are subjected in stubble fields are higher than the observed climatologic temperatures. The upper temperature limit of activity of the insect reported from laboratory investigations is therefore higher than the upper limit of activity as reported from comparisons of the distribution of the insect with that of climatologic temperatures.

Construction of Temperature Graphs.—In order to form a judgment concerning the length of time favorable to the activity of the weevil at any climatologic station it was necessary to put the ordinarily published monthly means of temperature into a form in which time intervals between the dates of attainment of critical temperatures might be read with a nominal accuracy of one day. To this end mean temperatures were plotted by months on coördinate paper[6] on which the axis of abscissas is divided into single days. Abscissas of the monthly means were the middles of the successive months. Continuous smooth curves were then drawn with reference to these plotted points in such a manner that the mean temperature of any month represented the mean ordinate of the curve drawn through the segment of the chart corresponding to the month in question. Such smooth curves are of course only an approximation to curves of mean daily temperature but are as close approximations as may be obtained for all but exceptional climatologic stations. From such curves the approximate mean daily temperature of any day in the year

[6] Coördinate paper by Keuffel and Esser no. 358–142 was used for this study.

and the interval in days between the attainment of any pair of critical temperatures may be read.

Even an approximation to the mean temperature of any day takes no account of the daily range of temperature. Yet the daily range of temperature is of great importance in an investigation of such an insect as the alfalfa weevil, particularly in fixing a date for the beginning of its activity in late winter or early spring. This insect has no definite period of hibernation, but becomes active in the warmer hours of the day even when the mean temperature of the day would indicate that it remains inactive. In order to take account of this peculiarity of the insect, use was made of mean maximum temperatures as well as of mean temperatures. On the temperature chart drawn for each station curves of mean maximum temperature were drawn in the same manner as of mean temperature. The temperature interval represented by the vertical distance between the two curves at any date is then approximately half the daily range on that date, and if the daily march of temperature be considered symmetrical, 12 hours have temperatures between the mean and the maximum.

A horizontal line was then drawn on the chart at a temperature of 12.5° C (54.5° F). The beginning of the period of activity of the weevil in the spring was taken as the date corresponding to the point on this horizontal line that is equidistant vertically from the curves of mean temperature and mean maximum temperature. Again assuming a symmetrical daily march, this is the first date in the spring when the temperature is above 12.5° C during 6 hours of the day. The end of the active period in autumn was fixed in the same manner. In figures 5 to 9 the segments of both temperature curves lying within the period of assumed activity of the weevil are drawn; the graphs are cut off on the left and on the right at the extremities of the season of activity in the graphs referring to stations where winter temperatures fall low enough to produce a winter interruption.

In fixing the limits of the period of activity of the weevil that are determined by high temperature, mean temperature alone was used; where a summer interruption of activity is indicated in figures 5 to 9, it begins where the rising curve of mean temperature reaches the ordinate of 25° C (77° F) and ends where the curve falls below this ordinate. This procedure implies that the weevil becomes inactive when 12 hours of the daily period (assuming a symmetrical daily march) have temperatures above 25° C. Before this point is reached, however, the activity of the adult weevil is certainly greatly reduced. When the beginning and end of the parts of the year during which temperature permits the adult

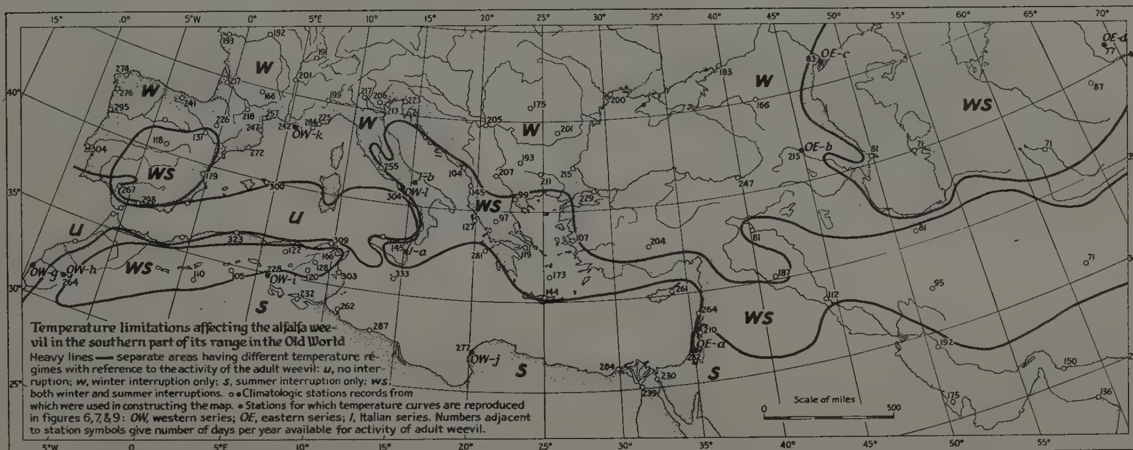

Fig. 2.—The four types of temperature regime under which the alfalfa weevil exists in the Old World. The small letters on the map that accompany the different series, such as the "*a*" in "*OW-a*," refer to the stations shown in figures 6, 7, and 9.

weevil to be active were thus fixed, it was easy to scale off from the chart the length of the period of activity in days.

Classification of Climatic Types.—The classification of types of annual

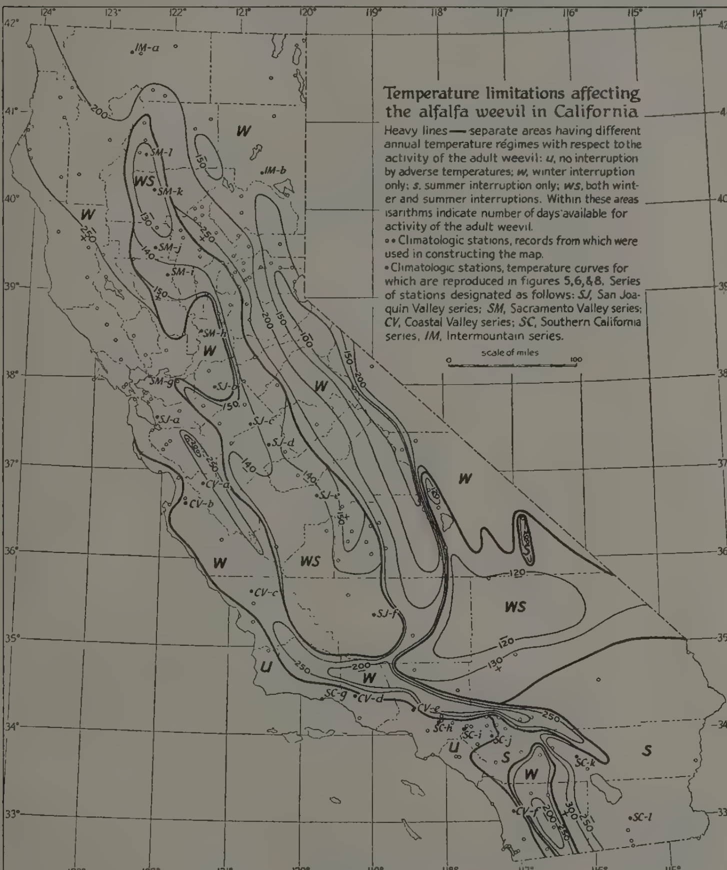

Fig. 3.—The four types of temperature regime in California under which the alfalfa weevil exists. The small letters on the map that accompany the different series, such as the "*a*" in "*SJ-a*," refer to the stations shown in figures 5, 6, and 8.

march of temperature given below, and the regional distinctions shown in figures 2 and 3, are based on the procedure just described, a chart having been drawn for each of the several hundred stations identified on the two maps. In figures 5 to 9 sections of a few of the charts are reproduced,

which are cut off on the time axis at the beginning and end of the periods that may be considered favorable to the weevil, and on the temperature axis by the ordinates of 12.5° and 25° C. Data were accessible to permit a detailed representation of temperature regimes in California, but only for a much less detailed representation of the parts of the Old World to be compared with California. The length of the period available for the activity of the adult alfalfa weevil is therefore represented on the map of California, figure 3, by isarithms[7] of number of days, but in figure 2 only by numbers entered next to the station symbols.

Within the range of distribution of the alfalfa weevil four types of annual temperature regime are distinguished: (1) Type *u* has no interruption of activity of the weevil in the course of the year; that is, the winter temperatures do not go low enough nor the summer temperatures high enough to exceed the limits defined. (2) Type *w* has winter interruption only. (3) Type *ws* has both winter and summer interruptions. (4) Type *s* has summer interruption only.

In type *u* the length of the annual period of activity is obviously 365 days. In types *w* and *s* the length of the annual period entered in figures 2 and 3 is the total number of days during which temperatures remain between the limits assumed to be critical for the weevil. In type *ws* there are two periods that fall within these limits, one in the spring and one in the fall. Since the spring period is of greater significance, the length of the period of activity in days, shown in figures 2 and 3 in the areas marked *ws,* is the length of the period of activity in spring and early summer. This is not intended to imply that the fall period is of no importance, for the sexual organs of the weevil are probably undergoing slow development at that time. To what extent this occurs is unknown, because the weevil has not been studied by us where there is a marked summer interruption. But there is not a great deal of activity during fall, and if the spring and fall periods were added to calculate the annual period of activity, the total would not be comparable with that in areas where there is no summer interruption. It would seem, however, that the fall period would become increasingly important as the summer interruption becomes shortened and the winter interruption lengthened.

It is doubtful whether any simple expression of temperature derived from ordinary climatologic records defines adequately the range of tolerance of any organism. The best that can be expected is that gradations of favorable or unfavorable conditions be defined and critical boundaries approximately located. We do not claim to have done more than that in

[7] *Editor's note.*—"Isarithm," sometimes spelled "isorithm," is a line drawn on a map or chart connecting points having equal numerical values of any quantity.

constructing figures 2 and 3. Since the quantities used in constructing the maps refer only to a range of temperature within which the alfalfa weevil can survive, and since the regional distinctions made are in terms of time rather than of temperature, extremes of heat and cold that kill the insect outright are not taken into consideration. These lethal conditions will be

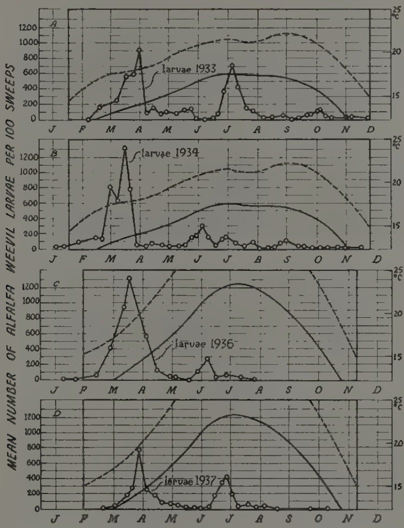

Fig. 4.—Average larval counts of the alfalfa weevil in the southern San Francisco Bay area in 1933 and 1934 and in the northern end of the San Joaquin Valley in 1936 and 1937, plotted for comparison with curves of mean (solid lines) and mean maximum (broken lines) temperature for two climatologic stations: *A* and *B*, Alvarado; and *C* and *D*, Stockton.

taken into account in the sections "Type *w* with Long Winter Interruption," "Type *ws* with Long Winters," and "Type *s* Climates Having a Summer Interruption but No Winter Interruption."

Relation of Larval Population to March of Temperature in Two Localities in Lowland Middle California.—The relation of the larval population in specific years to the average march of temperature in two localities in the infested area of lowland middle California is shown graphically in figure 4. The temperature curves drawn in *A* and *B* of figure 4 refer to Alvarado, a station near the eastern shore of the southern arm of San Francisco Bay; those in *C* and *D* to Stockton, situated at the northern

end of the San Joaquin Valley. Alvarado has the characteristic cool summers and mild winters of the Bay area; Stockton has a more continental annual march of temperature but one less extreme than is found farther south in the San Joaquin Valley. The larval populations plotted in figure 4 are averages of all the larval counts obtained by sweeping a number of alfalfa fields in each of the two areas—the southern San Francisco Bay area and the northwestern San Joaquin Valley—the climates of which are represented by the temperature curves for the two stations.

Larval populations in the southern San Francisco Bay area in 1933 and 1934 are used because they represent conditions obtaining before the larval parasite *Bathyplectes curculionis* (Thoms.) was firmly established in the Bay area. In 1933 the winter was cold; in 1934 it was mild. In 1933 larvae were not found in the Bay area until well after the beginning of the season of activity of the adult weevil as defined by mean temperatures. In 1934 they were found before the beginning of the assumed period of activity. The average between the dates of first appearance of the larvae in these two years comes close to the average date of beginning of adult activity as defined. While the larval population is not large toward the end of the year in the Bay area, temperatures remain favorable for the development of the sexual organs of the adults. The larval curves for both years show that there at least two broods of larvae and that adults are reaching sexual maturity throughout the season of activity. Later peaks, after the first rise of the larval curve to a maximum, are probably greatly reduced by frequent cutting of the alfalfa. Moreover, after the first crop is harvested, the alfalfa in different fields is likely to be cut at different dates, so that the average larval populations plotted represent averages of counts made in fields where the alfalfa is in different stages of growth. Such an averaging eliminates pronounced maximums (other than the first maximum in the spring) that might appear if the later growth periods between cuttings were uniform for all fields and were as long as the period required for the first crop to mature.

In the northwestern San Joaquin Valley, the season of 1936 followed a mild winter, that of 1937 a cold winter. (In 1933 and 1934 the weevil populations in the San Joaquin Valley were very small.) Here again, the average of the dates of appearance of larvae in the two years falls at about the beginning of the season of activity as defined by mean temperatures at Stockton. In each of the two years a second peak in the larval curves indicates the occurrence of a second brood. But after this second maximum the curve drops to insignificant levels, which indicates that the summer temperatures of the northern San Joaquin Valley are more effective in restricting the activity of the adult weevil than are the lower

temperatures experienced at the same time of the year in the neighborhood of San Francisco Bay. The agreement found between the seasonal march of larval population and the annual march of temperature in these two districts in lowland middle California gives us confidence in our definition of limiting temperatures.

TYPE *u*, CLIMATES HAVING NEITHER WINTER NOR SUMMER INTERRUPTION

From what is known of the habits of the weevil, areas having an annual march of temperature such as type *u* should be very favorable for it. According to data available, the weevil is found in only one area having this type of climate; namely, the northwestern coast of Africa and the extreme coastal strip of the western Mediterranean area (see fig. 2). The march of temperature in this area is illustrated in figure 6, *g*, by the curve for Mogador, Morocco. Our information on the destructiveness of the weevil in this general area is scanty, but according to J. M. Mimeur,[8] the weevil is well distributed throughout Morocco and causes damage only locally and occasionally. This fact would lead us to believe that there are factors other than climate that limit the activity of the insect. Possibly a climate of this type is very favorable to the parasites of the weevil. Or the brood or broods of the insect may be so dispersed through the year as to minimize its destructiveness.

A fairly large area lying entirely in southern California has a climate that falls into type *u* (see fig. 3 and fig. 5, *d* to *j*). Here, however, winter temperatures are lower and summer temperatures higher than in coastal Morocco, and at the present time the weevil is not known to occur in this area in California.

TYPE *w*, CLIMATES HAVING A WINTER INTERRUPTION BUT NO SUMMER INTERRUPTION

In the United States and over a large part of the Old World the weevil is most likely to be destructive in climates that fall into type *w*. It comprises a rather large variety of climates, and over a wide range of these the weevil finds conditions favorable. It can be roughly divided into two subtypes. The first has a relatively short winter interruption; the second, a long winter interruption.

Type w with Short Winter Interruption.—The first subtype of *w*, characterized by a short winter interruption, is found over a large part of central coastal California (fig. 3 and fig. 5, *a* to *c*) and in some places about the Mediterranean (fig. 2, fig. 6, *l* and fig. 7, *a*). This is the type of

[8] Letter to A. E. Michelbacher, April 28, 1938.

climate found in the infested area of lowland middle California in the several counties adjacent to San Francisco Bay and in the northwestern San Joaquin Valley. Much alfalfa is produced in this infested area, and

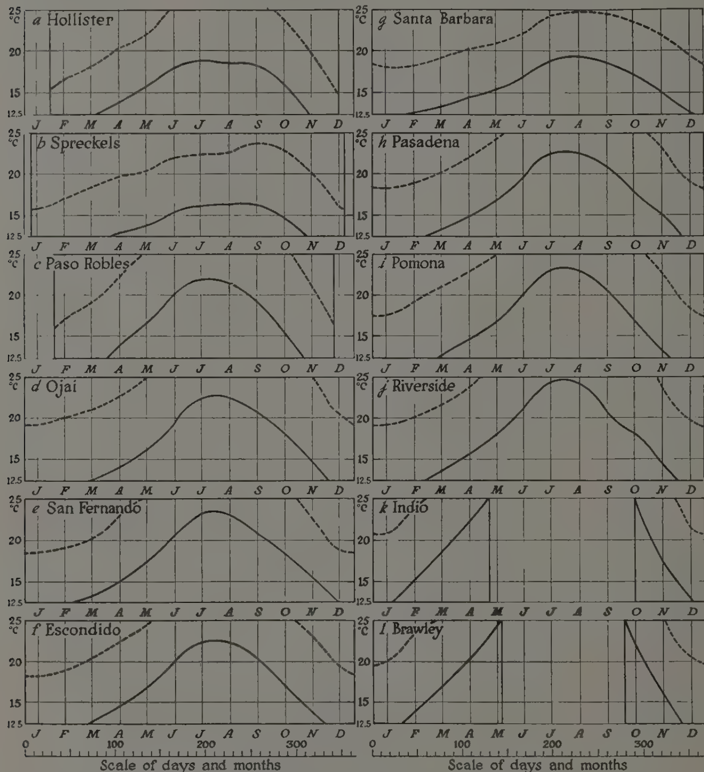

Fig. 5.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, stations in coastal valleys in the southern half of California (designated *CV* in fig. 3) in order from north to south; *g* to *l*, stations in southern California (designated *SC* in fig. 3) in order from the coast inland to Imperial Valley.

adjacent to it are other large alfalfa-growing sections. There is some variation in climate over the area, in terms of the length of the winter interruption. Near San Francisco Bay the winter interruption is very short, and summer temperatures are rather low; except for the short

winter interruption the annual march of temperature is similar to that of type *u* (compare Alvarado, fig. 8, *a;* Mogador, fig. 6, *g;* and Santa Barbara, fig. 5, *g*). In the northwestern San Joaquin Valley, on the other

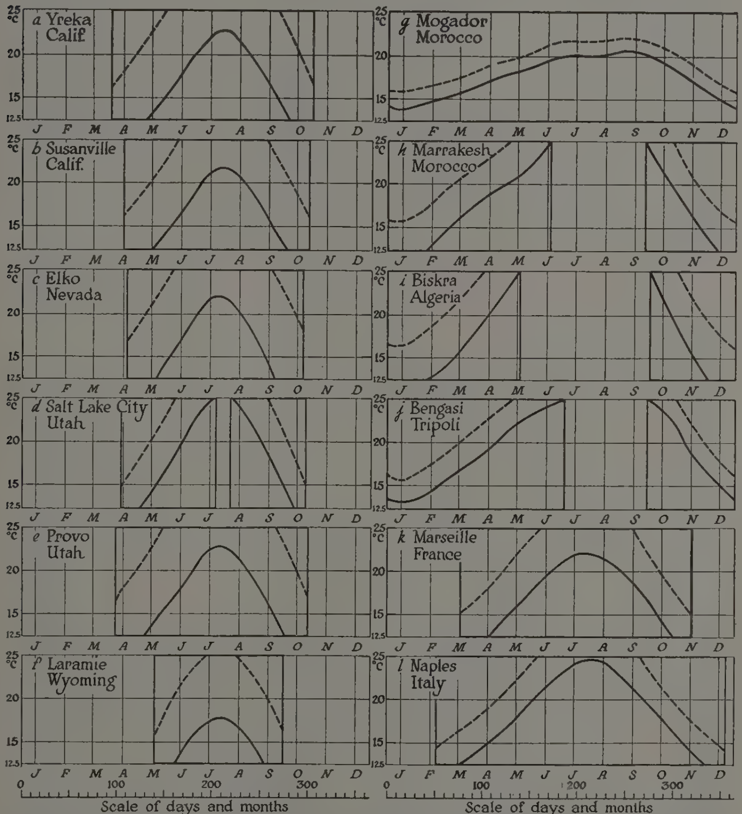

Fig. 6.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, intermountain series (the two California stations designated *IM* in fig. 3); *g* to *l*, western Old World Series (designated *OW* in fig. 2).

hand, the winter interruption is longer and the summer temperatures higher; its climate grades into type *ws*, characterized by both a winter and a summer interruption.

The weevil must have been present in lowland middle California for many years before its discovery in 1932, since when first found it was

already distributed over a rather wide area traversed by two ranges of hills. One of these ranges, the Altamont Hills, is rather wide and barren. Yet before the discovery of the insect (made accidentally) not a single complaint had been received of any damage done by it. Our observations of the alfalfa weevil have been limited to the seven years it is known to have been present in lowland middle California. Owing to differences in climate, the behavior of the weevil has been different here from what it has been in other parts of the United States where it occurs—specifically in the Great Basin. This behavior is probably not, however, much different from its behavior in parts of the Old World.

Near San Francisco Bay the weevil probably reacts to climatic condi-

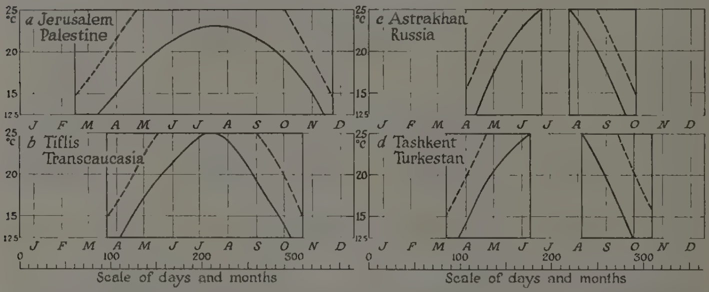

Fig. 7.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: eastern Old World series (designated *OE* in fig. 2).

tions in much the same way as it does along the northwestern coast of Africa and in the western Mediterranean area. There it is reported as doing damage only locally and occasionally, which report agrees with our observations here. Before the establishment of *Bathyplectes curculionis,* one severely damaged field could usually be found each year and sometimes several. Since the parasite became established, even these small losses have been greatly reduced, but possibly when final equilibrium is reached between the parasite and the weevil, fields will occasionally be found that have been damaged.

In the northwestern part of the San Joaquin Valley very little damage has been observed. In fact, unless the weevil had been rather closely observed, the conclusion could easily enough have been reached that it is not a pest. The climate here is very similar to that found in parts of Italy and Palestine. This fact is rendered evident by a comparison of the temperature curves for Stockton (fig. 8, *b*), with those for Naples (fig. 6, *l*) and for Jerusalem (fig. 7, *a*). The response of the weevil to climate in all the

areas represented by these stations must be rather similar. Bodenheimer (1930) reported that the weevil was present in Palestine, but that it was not considered a serious pest. Bodenheimer has, however, recently written[9] that since 1930 a more careful study of the weevil has been conducted and that it has been found to be a more serious pest than it was at first thought to be. Such an observation appears to agree rather closely with the observations made in lowland middle California. Certainly the weevil should not be considered a serious pest in the San Joaquin Valley. Since 1933, when the observations began, really serious injury has been noted in only one field, although in several others damage to the first crop has been noticeable. Injury may occur in one field while other fields in the same locality are relatively free from the insect. It has not been uncommon to find the density of the weevil in a heavily infested field ten or more times as large as in adjoining, more lightly infested fields.

At the southern edge of the infested area in the San Joaquin Valley only very light infestations have been encountered. The weevil was found near Gustine, Merced County, as early as 1933, but has always been scarce. No doubt it is encountering here a climate not very favorable to its development. The annual march of temperature near Gustine, probably very similar to that at Denair (fig. 8, *c*), represents the southern extremity of climates in the San Joaquin Valley that have, according to our interpretation, a winter interruption but not a summer interruption of activity of the adult weevil. Farther south summer temperatures become higher and the summer interruption appears (fig. 8, *d* to *f*). The same transition appears in the Sacramento Valley in a south to north direction (fig. 8, *g* to *l*). The difference in latitude between the southern San Joaquin Valley and the northern Sacramento Valley (compare Bakersfield, fig. 8, *f*, with Redding, fig. 8, *l*) expresses itself more distinctly in the length of the winter interruption than in the length of the summer interruption.

Type w with Long Winter Interruption.—The second subtype of *w*, characterized by a long winter interruption, is found in the intermountain region of the United States, including northeastern California (fig. 6, *a* to *f*). Representative stations in the Old World are Marseille, France, (fig. 6, *k*), and Tiflis, Transcaucasia (fig. 7, *b*).

In the United States the weevil reaches its highest degree of destructiveness in climates of this subtype. It produces a single and rather even brood. Egg deposition tends to occur within a relatively short period, so that the larvae attack the alfalfa in large numbers at the same time. This mass feeding is the principal cause of serious injury to the alfalfa.

[9] F. S. Bodenheimer, letter to A. E. Michelbacher, April 13, 1938.

This climatic type extends to the northern limit of distribution of the weevil in the United States, which limit is set by severe winter temperatures that persist for several months. Laramie, Wyoming (fig. 6, *f*), lies

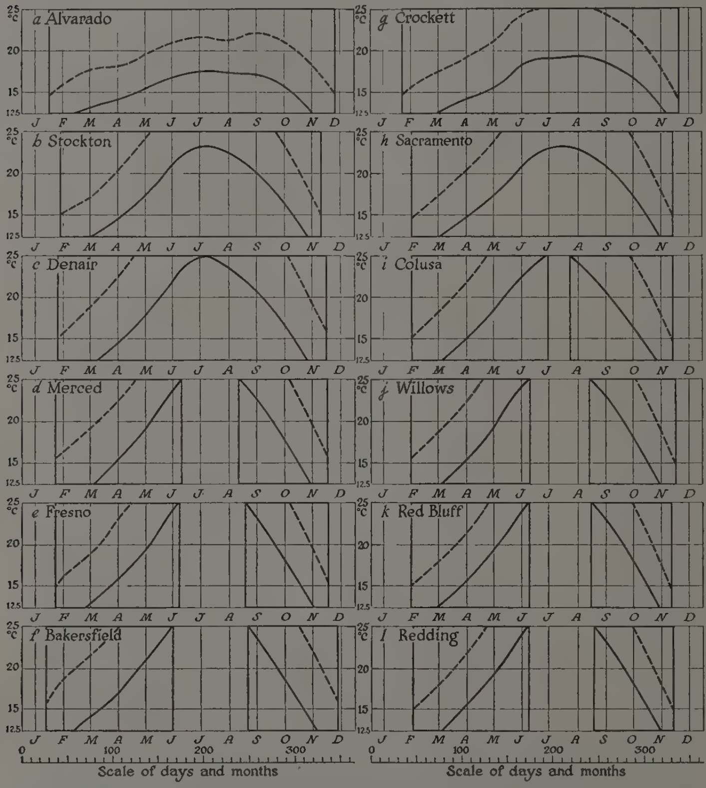

Fig. 8.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, San Joaquin Valley series (designated *SJ* in fig. 3); *g* to *l*, Sacramento Valley series (designated *SM* in fig. 3). The order of the stations in each series is from the San Francisco Bay area (Alvarado is not in the San Joaquin Valley proper) up to the respective valleys and so in the direction of increasing continentality.

about at this limit in the United States. In such an area the long severe winter reduces the time favorable to the weevil to a point where the pest is unable to survive. Even in areas subjected to serious weevil attack, cold winters lessen the damage done in the succeeding seasons. Reeves (1927),

writing of the Great Basin, stated that during the first nine years of the history of the weevil in America it was very destructive and that during this time temperatures were for the most part abnormally high throughout the egg-laying season in April and May. He observed the same conditions in later years when serious damage was done by the insect.

TYPE *ws*, CLIMATES HAVING BOTH A WINTER AND A SUMMER INTERRUPTION

Climates of type *ws* are found throughout the greater part of the interior lowlands of California (fig. 3 and fig. 8, *d* to *f* and *i* to *l*). The type is continental rather than coastal, and in the Old World appears along the northern shore of the eastern, more continental, basin of the Mediterranean, in the Near East, and in the Aralo-Caspian depression (fig. 2, fig. 7, *c* and *d*, and fig. 9). It, too, can be divided into two subtypes. One subtype has long and moderately severe to very severe winters; the other has rather mild winters.

Type ws with Long Winters.—The first subtype of *ws*, characterized by long winters, is found in the Aralo-Caspian depression (see graphs for Astrakhan and Tashkent, fig. 7, *c* and *d*). Both stations have long and severe winters and also summers sufficiently warm to produce, according to definition, a summer interruption of activity of the weevil. The nearest to these among the American stations represented is Salt Lake City (fig. 6, *d*), where, however, the summer interruption is very short. In the American Great Basin, however, the winters are not so cold nor the summers so hot as in its counterpart in the Old World.

Yakhontov (1934) reports that the alfalfa weevil is not a serious pest about Astrakhan. From a comparison of winter temperatures at Astrakhan with those at other continental stations, both in the United States and in the Old World (table 1), the weevil should not be expected to be serious; Astrakhan's winter temperatures must be close to the lower limit endured by overwintering adult weevils. This evidence is of no great value, however, since the same low winter temperatures reduce the cultivation of alfalfa itself to insignificance. In Turkestan, however, the weevil is a serious pest. Tashkent, our representative station for Turkestan (table 1), has notably milder winters than Astrakhan. Our conclusion, therefore, is that in climates of this subtype of *ws*, severe winter temperature is the critical factor that limits activity of the alfalfa weevil. Detailed observations of the behavior of the weevil have not been made in climates of this subtype in the United States.

Type ws with Mild Winters.—This subtype of *ws*, characterized by mild winters, is found in the San Joaquin and Sacramento valleys (fig. 8,

TABLE 1

COMPARISON OF TEMPERATURES IN AREAS WHERE THE ALFALFA WEEVIL IS A PEST WITH THOSE WHERE WINTERS ARE TOO SEVERE FOR ITS SURVIVAL

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Astrakhan,* U.S.S.R.	−7.00	− 4.3	−6.3	−3.2	−0.3	4.3	9.3	14.4	22.8	26.9	25.5	29.6	23.7	28.4	17.6	21.8
Tashkent, Turkestan	− 1.30	3.6	1.6	7.0	8.0	13.4	14.3	19.8	25.8	32.4	27.6	34.6	25.4	33.3	19.5	28.0
Tiflis, Transcaucasia	0.00	4.2	2.5	7.0	6.6	11.8	11.8	16.2	21.4	26.8	24.5	30.1	24.1	30.0	19.2	25.0
Laramie,* U.S.	−5.40	0.6	−4.9	0.8	−1.3	4.8	3.2	9.8	13.7	21.5	17.3	25.1	16.6	24.4	12.0	19.9
Provo, U.S.	−3.11	3.6	0.0	7.0	4.8	12.3	9.3	18.1	18.1	28.7	22.3	32.8	21.1	31.8	15.8	26.6
Salt Lake City, U.S.	−1.60	2.6	1.0	5.2	5.3	10.3	9.9	15.3	19.7	26.3	24.5	31.3	23.7	30.2	18.0	24.5
Elko, U.S.	−4.70	3.7	−1.5	6.5	3.0	11.5	7.3	16.1	17.1	27.3	21.4	33.1	19.9	31.7	13.9	25.8
Susanville, U.S.	−0.90	4.2	1.5	7.6	4.7	11.3	8.6	16.3	16.9	25.8	21.2	30.6	20.5	29.7	15.7	24.3
Yreka, U.S.	1.00	6.6	3.8	10.1	6.4	14.0	9.4	18.1	17.8	28.1	22.0	33.1	21.2	32.2	16.2	26.6

* Areas having too severe winters for the survival of the weevil.

d to *f* and *i* to *l*) and in Italy (fig. 9). Information on the behavior of the weevil in this subtype is rather meager. The insect is reported as being present in parts of southern Europe belonging to this subtype, notably in Italy. Little information is available on the amount of damage it does, although Martelli (1911) reported extensive damage done by the pest in 1909 at Campobasso in east-central Italy. Lucas (1849) reported the weevil as being taken in the following places in Algeria: Melah, near Lake Tonga, and in the vicinity of Lacalle. These places for the most part fall into the subtype being discussed. In California the weevil has not penetrated into any area having both a winter and a summer interruption although in the northwestern San Joaquin Valley there is no barrier between the area of present occurrence and the more continental part of

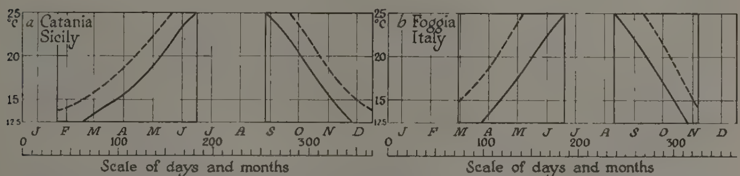

Fig. 9.—March of mean (solid lines) and mean maximum (broken lines) temperature during seasons permitting activity of the adult alfalfa weevil: Italian series (designated *I* in fig. 2). Compare figure 6, *l*.

the Valley. Winter and spring temperatures should be favorable in the parts of the interior valleys of California assigned to type *ws;* the only important element of the climate that might be detrimental is the hot, dry summer. Perhaps the length of time during which the weevil has been under observation in California is as yet insufficient to permit a definitive judgment concerning the distance it may be expected to penetrate into the more continental parts of the valleys. Yet evidence indicates that their climate is not very favorable to it and that there is not much likelihood of its becoming a serious pest in them. Apparently the long, hot summers increase the length of the diapause to a point where the environmental resistance becomes very great.

In figure 9 temperature curves for two Italian stations belonging to the second subtype of type *ws* are reproduced. They are very similar to the curves shown for interior stations in the San Joaquin and Sacramento valleys (fig. 8, *d* to *f* and *j* to *l*). The principal difference is that the maximum temperatures occurring in the summer are notably higher at the California stations (table 2). We therefore consider high summer temperatures the limiting factor in the second subtype of type *ws,* as low winter temperatures are in the first.

TABLE 2

Comparison of Temperatures for Stations in Southern Europe and in the Interior of the Sacramento and San Joaquin Valleys

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Catania, Sicily	10.80	13.6	11.4	14.2	13.5	16.0	15.7	18.6	23.4	26.7	26.4	30.1	26.3	30.1	24.4	27.5
Foggia, Italy	6.40	10.0	7.5	11.1	10.2	15.2	13.5	18.2	22.6	28.5	26.0	31.9	25.7	31.2	22.0	26.7
Merced, U.S.	7.80	12.8	9.8	16.4	11.8	19.1	15.2	22.5	23.6	32.5	26.9	36.1	25.9	35.1	22.5	31.3
Fresno, U.S.	7.83	12.4	10.8	16.3	12.9	18.9	15.9	23.1	24.1	32.9	27.7	37.2	26.9	36.3	23.0	31.7
Bakersfield, U.S.	8.40	14.7	11.4	18.8	13.7	21.3	17.0	24.7	25.3	34.5	28.8	37.9	27.6	37.1	23.3	32.9
Willows, U.S.	7.40	11.7	9.7	15.5	12.2	18.5	15.2	22.3	23.9	32.5	26.9	36.1	26.1	34.7	23.0	30.7
Red Bluff, U.S.	7.33	11.6	9.9	14.8	12.3	17.8	15.2	21.4	23.9	31.4	27.5	35.9	26.5	35.1	22.8	30.4
Redding, U.S.	7.30	12.1	9.7	14.9	12.2	17.9	15.4	21.9	24.0	31.3	27.7	35.8	27.1	35.2	23.1	30.5

TABLE 3

Comparison of Temperatures for Stations in North Africa and Imperial Valley

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Marrakesh, Morocco	11.4	15.8	12.9	17.9	16.1	20.6	18.8	22.4	24.5	30.4	28.0	34.8	30.3	36.2	24.9	30.0
Biskra, Algeria	10.7	16.6	13.1	18.8	15.5	21.4	19.9	25.6	29.9	35.7	34.6	40.3	32.8	39.0	29.1	34.7
Bengasi, Tripoli	13.2	15.8	14.4	17.5	16.7	19.9	19.1	22.6	23.9	27.0	25.6	28.3	26.2	28.9	25.6	28.9
Indio, U.S.	12.1	20.9	15.1	23.8	18.3	26.4	22.3	30.1	31.0	38.9	34.1	41.4	33.3	40.8	29.9	38.1
Brawley, U.S.	11.4	20.1	14.1	23.3	16.9	25.6	20.4	29.4	29.1	39.2	32.3	41.1	32.0	40.6	28.4	37.8

TYPE *s*, CLIMATES HAVING A SUMMER INTERRUPTION BUT NO WINTER INTERRUPTION

Climates of type *s* are found in the Imperial Valley of California (fig. 5, *k* and *l*) and in northern Africa (fig. 6, *h* to *j*). The weevil is reported to occur throughout northern Africa. De Lepiney and Mimeur (1932) reported its presence in many localities in Morocco, including the vicinity of Marrakesh (fig. 6, *h*). Willcocks (1922) reported it from Egypt as a pest on berseem (Egyptian clover); but the rapid growth of the host plant, close feeding by cattle, or frequent cutting of the crop prevents it from causing appreciable damage. He reported further that he had seen only one or two instances of serious injury and that these were in fields where the clover was making a poor growth. A. E. Hassan[10] writes that the alfalfa weevil is present throughout the Nile Valley and is found in the oases of the western desert. He states that little alfalfa is grown in the area mentioned, but that he considers the weevil a serious pest especially during the breeding season from January to April. Fletcher (1917) reported the weevil as occurring in India at Pusa, Lyallpur, and in the Punjab but that it is not considered a pest. This area falls into type *s*.

In northern Africa injury by the weevil is probably for the most part restricted to areas close to the coast and at higher elevations. Certainly there are no published reports of its causing serious losses, nor should one expect to find it abundant in the hot, dry interior of northern Africa. Along the coast and at higher elevations lower summer temperatures obtain than in Imperial Valley (table 3) or, for that matter, in many other parts of southern California. In the interior valleys of southern California at any rate, the daily and yearly fluctuations of temperatures are much greater than in coastal northern Africa. These more extreme fluctuations are probably more hostile to the weevil than the temperature conditions under which it exists in northern Africa. We believe, therefore, that it will not be able to adapt itself to the climate of Imperial Valley and that even in localities having temperatures such as are observed at Riverside (fig. 5, *j*), which station just falls within type *u*, it will find survival rather difficult on account of the high summer maximums.

CONFUSION OF SPECIES

Recently (spring of 1939) *Hypera brunneipennis* (Boh.), a very close relative of the alfalfa weevil, *H. postica* Gyll., has been found in the Yuma Valley of Arizona and in the adjacent part of California. The two

[10] Letter to A. E. Michelbacher, April 18, 1938.

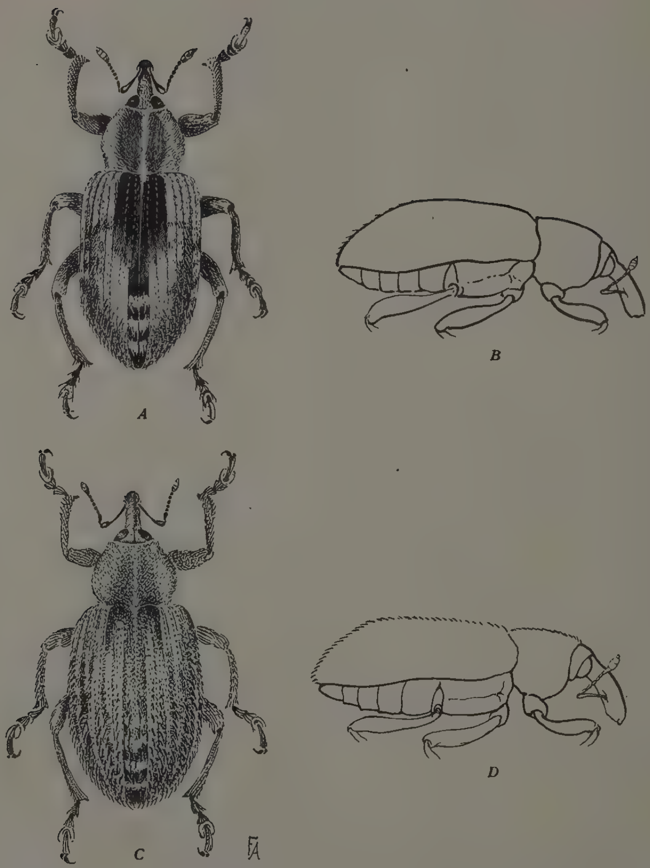

Fig. 10.—*A*, Dorsal view, and *B*, lateral view, of the adult alfalfa weevil, *Hypera postica* Gyll.; *C*, dorsal view, and *D*, lateral view, of adult *H. brunneipennis* (Boh.).

species are very much alike[11] (see fig. 10), but *H. brunneipennis* is larger with proportionately broader prothorax, is flatter in side view, has a more even and not so pronounced color pattern, slightly more erect setae, and the elytra is broader, evenly oval, and not so parallel in front as in *H. postica.*

[11] The authors are indebted to Professor E. C. Van Dyke for the comparisons of the two species as here given.

Hypera brunneipennis, known by the common name of Egyptian, or Ethiopian, alfalfa weevil, is reported from Egypt and Sicily (Schoenherr, 1834; Csiki, 1934). It is probably widespread in northern Africa although it is not known to occur in Europe, for Capiomont (1868) stated that all specimens labeled as *brunneipennis* were *H. murina*. He gave the distribution of *brunneipennis* as Egypt, Abyssinia (Ethiopia), and Hindustan. Very probably it has been mistaken, in part, for *H. postica* and referred to that species in the literature dealing with the occurrence of the alfalfa weevil in Africa. Both species occur in northern Africa,[12] but because *H. brunneipennis* is an insect apparently well adapted to climates having hot summers, it no doubt extends into the hotter regions. Because it is already found in Yuma Valley, there is little doubt that it will find the Imperial Valley and other desert regions with hot summers where alfalfa is grown suitable for its survival. Recently specimens have been received from Egypt, which M. T. Sayed[13] reports as being the common species occurring there.

In reply to an inquiry about the distribution of *Hypera postica,* L. L. Buchanan writes the following:

> As far as I can find, the National Museum Collection [Washington, D. C.] contains no specimens of *Hypera postica* from northern Africa, India, Persia, or any of the neighboring Asiatic countries. It should be remembered, however, that the Museum Collection from these regions is relatively very limited, and the absence of a species does not necessarily have any significance.
>
> In looking over the undistributed and unarranged material I did find a few specimens of *Hypera* which were previously overlooked and which may be of some interest to you. One of these is supposedly from Syria, and bears a label "*ponticus* Cap."; it seems to me to belong to *Brunneipennis* Boh. A set of five specimens are from Mostaganem, Algeria, and are labeled "Algerian variety of *Ph. varius*"; these I feel confident are *Hypera murina* F., a species which rather closely resembles *brunneipennis* but has a somewhat differently shaped prothorax, different ♂ genitalia, etc. Lastly, a few unidentified specimens from northwestern India (labeled "Punjab and U. Provinces") were located. These agree very well with *brunneipennis*.[14]

PARASITISM AND CLIMATE

Parasitism must be taken into account in any discussion of the climatic limitations of the alfalfa weevil. Climatic conditions favorable to the weevil may also be exceptionally favorable for one or more of its parasites. It is therefore conceivable that the weevil may be more destructive,

[12] Specimens of *Hypera postica* were received from Le Kef, Tunisia, during the winter of 1939 (after this paper went to press), so there can be but little doubt that this species exists throughout the cooler regions of northern Africa. Also during 1939, specimens of *H. postica* have been received from several localities in Palestine.

[13] M. T. Sayed, letter to A. E. Michelbacher, August 31, 1939.

[14] L. L. Buchanan, letter to A. E. Michelbacher, July 17, 1939.

or at least more abundant, in a climatic zone other than its optimum if the conditions in the zone in question are not optimum for maximum parasitism. Nicholson (1937) has cited this principle, but without giving any examples of its application.

In California our observations have yielded evidence of such a phenomenon. When the weevil was first found in lowland middle California, it was most abundant at Pleasanton, Alameda County, and in adjacent areas near San Francisco Bay. The populations encountered in the infested part of the San Joaquin Valley were rather small in comparison with those found near the Bay. In 1933 and 1934 the United States Department of Agriculture Bureau of Entomology and Plant Quarantine introduced the larval parasite, *Bathyplectes curculionis* (Thoms.), into the infested areas. The parasite readily became established and is evidently more effective about Pleasanton and in the Bay area in general than in the San Joaquin Valley.

As a result of depredations of the parasite, the weevil populations now found in the Bay area are smaller than those found in northwestern San Joaquin Valley, a condition that is the reverse of that which obtained before the parasite was introduced. The relation of the parasite to the weevil is discussed by Michelbacher (1940). Further observation is needed to determine whether the present relative frequency of the insect in the two areas will be permanent. If the trends of the weevil populations were studied without any attention to parasitism, however, the conclusion might be reached that the climate of the northwestern part of the San Joaquin Valley is more favorable to the weevil than that of the areas close to San Francisco Bay, with their cooler summers and more moderate winters. Such is evidently not the case.

We have noted that the maximum destructiveness of the weevil has been observed in areas having rather short growing seasons, such as the Great Basin and Turkestan. Short growing seasons tend to bring about mass feeding by weevil larvae with resulting heavy losses. It has been suggested that in more moderate climates, such as those about San Francisco Bay and in the western Mediterranean, the destructiveness of the weevil has been slight because the brood or broods are scattered and drawn out over a long season of activity, so that there is not the same opportunity for mass attack as in climates having a shorter season of activity. Reeves (1917) reported that H. S. Smith, who studied the weevil along the coast of Italy, was of the opinion that one of the reasons why the weevil, though present in considerable numbers there, is of no consequence as a pest is that the generations are more or less spread out so that feeding continues through several months instead of being concen-

trated into a few weeks. Certainly, in climates having mild winters and cool summers, feeding continues through a good portion of the year, partly because the lifetime of a single generation is prolonged, and partly because the climate permits more than one generation a season. However, even under such conditions some damage may be done by the weevils attacking the alfalfa en masse.

A mild summer and a long season of activity may not only favor a certain parasite but may also favor parasitism in general because the host is accessible through a large portion of the year and parasitism therefore probably more effective.

SPREAD OF THE ALFALFA WEEVIL IN LOWLAND MIDDLE CALIFORNIA

In spite of the fact that the southern limit of infestation cuts across one of the most important areas of alfalfa production in the state, in seven years, as previously mentioned (p. 103), the spread of the weevil beyond the area found to be infested in 1932 has been slight. In 1933 the weevil was found about 2 miles northwest of Gustine, Merced County; this find represented an air-line extension of only about 6 miles since the preceding year. Since that time the weevil has shown no evidence of building up in population in the vicinity of Gustine; in some years it has been very difficult to find. In 1938 a few specimens of the weevil were collected near Hilmar, Merced County; this find established an extension of the area of infestation but did not carry the weevil south of where it had already been found for several years.

The greatest spread of the weevil has been eastward and northward, but no jumps of noteworthy magnitude have been recorded. In some places where the insect has been collected it has been very scarce. Quite possibly it existed in such places for some time before it was first collected, so that these finds may not record recent jumps. Yet conditions in the San Joaquin Valley would seem in general to be favorable to rapid spread of the weevil. Not only are quantities of alfalfa grown, but in some areas under favorable conditions there is a luxurious growth of bur clover (*Medicago hispida*), a very suitable host plant and one that should aid the weevil in its spread from one field to another.

Reeves (1927) reported the dispersion of the weevil at the rate of 10 to 20 miles a year, with little regard to natural aids or hindrances. Newton (1933) recorded that in Colorado it had spread at an average rate of about 6 miles a season. Hagan (1918) estimated an average spread of 20 miles a year but was of the opinion that under very favorable conditions the rate might be as high as 50 to 60 miles.

If the weevil had spread in the San Joaquin Valley at the rate of only 10 miles a year, it should now be found at least 60 miles from the boundary of the infested area as determined in 1932. The greatest spread observed is hardly half this distance, and the spread south in the San Joaquin Valley is not more than a tenth of the distance in spite of the fact that the southern periphery of the known infestation is in the midst of a large alfalfa-growing section. Since, in spite of apparently ideal conditions for rapid dissemination, no such dissemination has taken place, we judge that the insect is reaching an unfavorable climatic zone. We have suspected this since the time when the weevil was first discovered in the San Joaquin Valley, but because of the large populations observed in scattered fields throughout the infested area from Tracy, San Joaquin County, to Patterson, Stanislaus County, we have not felt justified in drawing definite conclusions before the insect was observed through a series of years. Small populations occur throughout the infested area, but only in scattered fields does the population rise to a level at which some injury results.

In the spring of 1939[15] the larval population was the largest yet encountered in the San Joaquin Valley. In most fields an increase in numbers over the preceding year was observed, and in several the injury done, bordered on economic damage. Yet in spite of this general increase in population we were unable to demonstrate any extension of the infested area.

The most serious damage observed was in a single field near Patterson, Stanislaus County. Although this field is situated not far from the southern boundary of the infestation, the first crop of alfalfa in 1936 was almost completely destroyed. The infestation was so heavy that the growth of the second crop on half the field was delayed four weeks. This occurrence was unusual; but if such a population can develop near the southern border of the infested area, it is difficult to understand why the weevil is not able to penetrate farther south in the San Joaquin Valley. Nevertheless, no marked jumps have been noted; and over the infested area as a whole it is difficult to find fields in which the insect is actually doing damage.

Failure of the weevil to advance farther southward is a curious phenomenon which may, nevertheless, have a parallel along one part of the boundary of its distribution in the Old World: in Turkestan, U. S. S. R. —represented in our collection of temperature curves by Tashkent,

[15] During the spring of 1940 (after this paper went to press) a serious outbreak of the alfalfa weevil occurred in 5 or 6 fields just south of Tracy. Outside of this one small area of heavy infestation the weevil population was very small, being no larger than in previous years and in some cases smaller.

figure 7, *d*. On the basis of our analysis of its temperature limitations in the United States, the weevil should not exist here at all, and in fact this area is certainly close to both the northern and southern boundaries of weevil distribution in central Asia.[16] Yet the weevil not only survives, but even inflicts noteworthy damage in this area. Here then, as in the San Joaquin Valley of California, large weevil populations are apparently built up very close to a climatic barrier. That the insect should be more destructive near such a barrier than in the climates presumably most favorable to its survival is a strange paradox. As a further, though less striking, example, perhaps the Great Basin may be compared with lowland middle California. We merely note this paradox, without trying to offer a complete explanation. Our information, both on the behavior of the weevil and on the temperatures that obtain along the boundaries of the Asiatic area of infestation, is too scanty to permit us to discuss the favorable and unfavorable conditions encountered there by the weevil.

The conclusion that climate limits further rapid spread in the San Joaquin Valley could be more easily accepted if the weevil had shown signs of more rapid dissemination about the country adjacent to San Francisco Bay, where summers are cool. All evidence indicates that the climate in the Bay area is very favorable. The failure of the weevil to spread more rapidly than it has may be the result of scarcity of alfalfa fields, but this fact by itself hardly seems an adequate explanation. The larval parasite, *Bathyplectes curculionis*, may also be a factor.[17] The fact

[16] The weevil is, in fact, absent from most of the Aralo-Caspian depression, evidently on account of the shortness of the season favorable to its activity between the cold winter and the hot summer. Yakhontov's (1934, fig. 3, p. 32) map shows the weevil as occurring in Turkestan only in the foothill country at the eastern edge of the Aralo-Caspian depression. The northern boundary, according to Yakhontov, swings sharply southeastward from the vicinity of Leningrad to the mouth of the Volga, is resumed at the northeastern extremity of the Caspian Sea, and extends eastward through Kazakstan to Lake Balkhash. The more southerly position of the boundary in the east is the consequence of the increasing severity of winter temperatures toward the interior of the continent. Summer temperatures become higher, as well, toward the eastern extremity of the boundary, both because of increasing continentality and because of lower latitude.

[17] On April 11, 1940 (after this paper went to press), a thorough survey was made south of the known infestation adjacent to the San Francisco Bay. Although no alfalfa weevils were collected, four adult *Bathyplectes curculionis*, the larval parasite of the alfalfa weevil, were taken—one near Paicines, San Benito County, the southernmost point covered in the survey. The finding of the parasites may indicate that the weevil occurs here but in such small numbers that it has not yet been taken; for the area surveyed has a climate known to be favorable for extremely efficient parasitism. If the weevil does occur here, then the area of the infestation has been increased in an air-line distance by more than 60 miles. Of course the specimens of *Bathyplectes* collected may possibly have flown into the area from the alfalfa-weevil-infested area to the north, and although we hardly believe this to be the case, doubt will exist until specimens of the alfalfa weevil are actually collected. If the latter really occurs in this area, then some interesting light is shed on the occurrence of the pest in lowland middle California. In 1932, after the discovery of the weevil, an ex-

remains, however, that the slow spread of the weevil in the Bay area weakens somewhat the hypothesis of a climatic cause for the lack of expansion of the infestation southward into the San Joaquin Valley. However, the fact that the weevil has hardly been able to maintain itself near Gustine would indicate that it is meeting considerable environmental resistance, and we believe this resistance to be high summer temperature.

PROBABLE FUTURE SPREAD OF THE ALFALFA WEEVIL IN CALIFORNIA

There is always danger in attempting to predict what an insect will do in a new area. The attempt to do so could be undertaken with full prospect of success only if the necessary information were available from all other areas in which it occurs. Even then there would be difficulty in predicting the behavior of the insect in a new home in the absence of its usual parasites and predators. But the climatic limitations of an insect should be capable of definition if its distribution in its original habitat and the climatic conditions it encounters there were thoroughly known. The information at our disposal concerning the distribution and abundance of the alfalfa weevil in the Old World, and concerning the climates of the wide area of its distribution there, has fallen far short of what we should have liked to have. Statements in the literature concerning the distribution and abundance of the insect are too often couched in extremely general terms. Climatic data, particularly on mean maximum temperatures, are scanty for many parts of the wide area of distribution of the insect, especially for sparsely settled and scientifically backward areas. We cannot be certain about the comparability of all the data we were able to find. The southern limit of distribution of the insect in the Old World has not been defined accurately, nor the extent of damage done by it in northern Africa. The tracing of this southern limit is further complicated by the occurrence of *Hypera brunneipennis* in the vicinity of the southern limit of *H. postica*. Nevertheless, with the information obtainable, and with our knowledge of the behavior of the weevil in California, we are in a position to say something concerning its probable

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tensive survey of lowland middle California was made, and since it was not found around San Benito County then, the supposition is that the weevil was first established in the San Joaquin Valley. From there it spread to the Pleasanton area and then to the fields adjacent to the San Francisco Bay. It probably had just recently reached the San Francisco Bay area at the time of its discovery in the San Joaquin Valley and therefore it had not had sufficient time to spread south, even though the climate was favorable to the pest. *Bathyplectes* was introduced into the San Francisco Bay area in 1934, and because it became such an effective parasite, and since there were no extensive further surveys beyond this area, the spread of the weevil was obscured.

future spread in this state and concerning the likelihood of its becoming destructive in the large fraction of the area of California to which it has not yet spread.

These conclusions are expressed in the following paragraphs, and the climatic areas referred to are drawn in figure 11. Figure 11 is based on the data shown in figure 3 and on a comparison of the distribution of the weevil in the Old World, for which the southern part of the area of distribution of the insect is analyzed climatically in figure 2. In addition, conclusions based on the considerations expressed in the foregoing independently of our treatment of the annual march of temperature have been used, particularly in making estimates of the expansion of the weevil in the parts of the state having high maximum temperatures in summer. Errors made here in the estimate of possible future expansion of the area of infestation are probably all in the direction of giving the weevil the benefit of any doubt of its ability to invade hitherto uninfested country. The potential spread defined is to be looked upon as a maximum rather than as a minimum estimate.

The weevil should be able to survive in all the coastal valleys of California. In some of these it may occasionaly appear in destructive numbers but should not in general become a serious menace to alfalfa production. In areas having moderate climates the larval parasite, *Bathyplectes curculionis,* may be very effective in holding the weevil populations in check. The weevil should be able to maintain itself in the cooler parts of southern California, but we doubt very much that it will be a serious pest. Here and there a small amount of damage may be done. The weevil should spread northward in the Sacramento Valley at least to a point a little north of Sacramento; within this potential area of infestation some injury may occasionally be experienced.

Extensive damage may be expected in all parts of the state having type *w* climate with long winter interruption similar to that in the intermountain region (fig. 6, *a* and *b*). Fortunately only a very small part of the alfalfa grown in California is produced in such climates.

Information gained from investigation of the weevil to date indicates that areas having summer temperatures as high as those observed at Denair (fig. 8, *c*) or higher, that is, belonging to type *ws* with mild winters and high summer temperatures, are safe from serious attack by the weevil. Hence large parts of both the San Joaquin and Sacramento valleys should be unsuited to the pest and not in danger of serious attack.

We have no way of judging the effect of very hot, dry summers on the weevil but are inclined to believe that they are very unfavorable and are an important influence in limiting the distribution of the insect in Cali-

fornia. The work of Sweetman and Wedemeyer (1933) showed that temperatures of 30° to 37° C are very injurious, especially when relative humidity is high. Since climatologic observations probably always record maximum temperatures lower than those actually experienced by the weevil among the plants on which it feeds, undoubtedly it would daily experience temperatures as high as Sweetman and Wedemeyer found injurious, especially in stubble, during the hot summers of the interior California valleys.

In figure 11 the heavier shading is used for the parts of the state in which greater damage from the alfalfa weevil may be expected. The first area, the one where the weevil is likely to be most destructive, is the part of the state having a type *w* climate with long winter interruption similar to that of the intermountain region. Although it covers a large fraction of the area of the state, it is of no great importance, since it is largely mountainous and only in small part suited to alfalfa culture.

The second is the coastal area; although it has a climate highly suitable to the weevil (*u* and *w* with mild winters), we do not expect the weevil to do serious damage there, because the study of the larval parasite *Bathyplectes curculionis* indicates that the climate of coastal California is also well suited to the activity of the parasite which will act as an important check on the weevil.

The third area includes the interior valleys of the state having only moderately continental climates, type *w* with moderately mild winters and higher summer temperatures than found in the coastal areas. This area includes a very large alfalfa-growing section. Under favorable conditions of culture the weevil may be somewhat destructive locally and occasionally in this area but will probably not become a serious pest. It is possible for the weevil to produce at least a partial second generation within a season. *Bathyplectes curculionis* does not appear to be as effective here as in the coastal area. Rapid growth and frequent cutting of the alfalfa are probably important factors in reducing damage by the weevil. The weevil is known to have been present in a part of the area since 1932, and during this time has not been a serious pest.

The interior valleys having hot summers (*ws* with high summer temperatures) make up the fourth area. The weevil has not penetrated into this area, but in the Old World it is reported from areas having a similar climate, so that on the basis of this evidence the spread into corresponding parts of California might be expected. But the situation is complicated by the fact that in the Old World the alfalfa weevil has evidently been confused in part with the closely related species, *Hypera brunneipennis*. This fact hampers our judgment concerning the possible future

spread of *H. postica*. Judgment seems warranted, however, that even if the alfalfa weevil does establish itself in this area it will never become a serious pest. *H. brunneipennis* will probably in time find its way into the

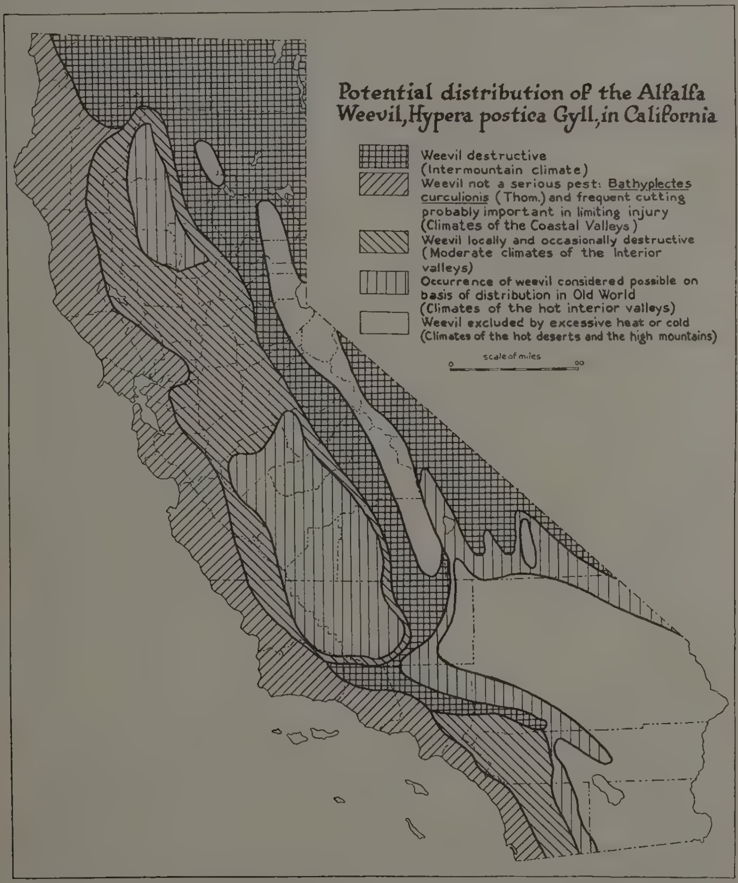

Fig. 11.—Greatest potential distribution of the alfalfa weevil in California.

area, and when it does, we expect that it will find the climate well suited to its development.

The fifth area shown in figure 11 includes both the higher mountain regions where the winter is too cold for the weevil to survive, and the hot deserts where high temperatures experienced through a good part of the

year exclude it. Three climatic types are included: *w* with short summer period of activity of the weevil, *ws* with short spring period of activity, and *s* with short winter period of activity. *Hypera brunneipennis* is already known to occur in the last type. In the very small infested area to which it was limited when first discovered in the spring of 1939, it was found in large numbers, and all our evidence indicates that *H. brunneipennis* will find the hot deserts of California very favorable to its survival.

SUMMARY

Because the alfalfa weevil has failed to spread readily into the hotter portions of the San Joaquin Valley since its discovery in lowland middle California in 1932, we are inclined to the belief that the pest is encountering a climatic barrier.

From our observations and from studies made throughout the world where the weevil occurs, it appears that high temperature sends the adult weevils into estivation. Furthermore, high temperature retards or inhibits the maturing of the sexual organs. The temperature range favorable for sexual development appears to fall between the limits of 10° and 25° C. Using this temperature range as a basis, the portion or portions of the year favorable to adult-weevil activity have been plotted for stations in America and in a part of the Old World where the weevil is known to occur. By so doing the weevil was found to exist in areas having four distinct types of climate: (1) type *u* in areas where temperatures favorable to adult activity are present throughout the entire year; (2) type *w* where, owing to cold winters, there is a winter interruption in adult activity; (3) type *s* where, owing to hot summers, there is a summer interruption; and (4) type *ws* where both cold winters and hot summers cause a summer and a winter interruption.

Areas having a winter interruption (type *w*) are further divided into two subtypes: (*a*) those having a short winter interruption; and (*b*) those having a long winter interruption. In climates of the latter type the alfalfa weevil is very destructive. This is the result of the short growing season which brings about a mass attack of the weevil on the alfalfa. Climates of this type are characteristic of the intermountain region of the United States which includes northeastern California. In this subtype the principal adverse factor affecting the weevil is low winter temperature. In climates of the first subtype where the winter interruption is short, adult weevils are active early in the year and before midsummer there is time for one full generation and at least a partial second generation. Alfalfa is seriously attacked only occasionally. This subtype ap-

pears in California in the coastal valleys north of southern California, in the lower extremities of the San Joaquin and Sacramento valleys, and along the coast of the northern half of the state.

Areas having both a winter and a summer interruption (type *ws*) are also divided into two subtypes: (*a*) those having cold winters; and (*b*) those having relatively mild winters. The first subtype is represented by the continental stations in the Old World where the alfalfa weevil is destructive because of mass feeding by the larvae, and the factor that limits the weevil is cold and severe winters. In the second subtype with mild winters the limiting factor is high summer temperatures, as is also the case in the climatic type *s* where there is a summer interruption but no winter interruption.

Judging from the reported distribution of the alfalfa weevil in the hotter portions of its range in the Old World, the pest can apparently adapt itself to almost all the climates of California. Certainly the climates of the hot California deserts would appear to be favorable, but we hardly think that this is the case, for evidence is presented that would tend to indicate that a second species closely related to the alfalfa weevil is involved. The species *Hypera brunneipennis* was recently found in the neighborhood of Yuma, Arizona, and adjacent part of California. Very likely this species, which is adapted to hot climates, has been confused with *H. postica* in the hotter portions of the Old World and has been referred to the latter species. Judging from the behavior of the alfalfa weevil in California and the lack of reported damage in places such as Italy, we are inclined to believe that the pest will not be able to survive in the hotter portions of California.

ACKNOWLEDGMENTS

It is with sincere pleasure that we express our appreciation to Mr. M. L. Jones, Associate Economic Entomologist of the State Department of Agriculture, for his valuable assistance in furnishing information on the results of the alfalfa-weevil surveys which he conducted throughout the state.

Thanks are due to W. P. A. project O.P. 665–08–3–29 (unit B–9) for the aid rendered in inking in the graphs and for the drawings of the two species of alfalfa weevil.

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